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ANIMAL ORIENTATION AND NAVIGATION

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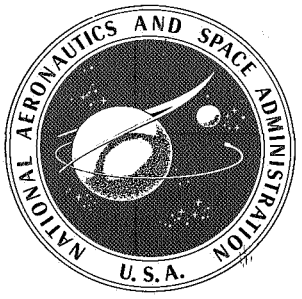
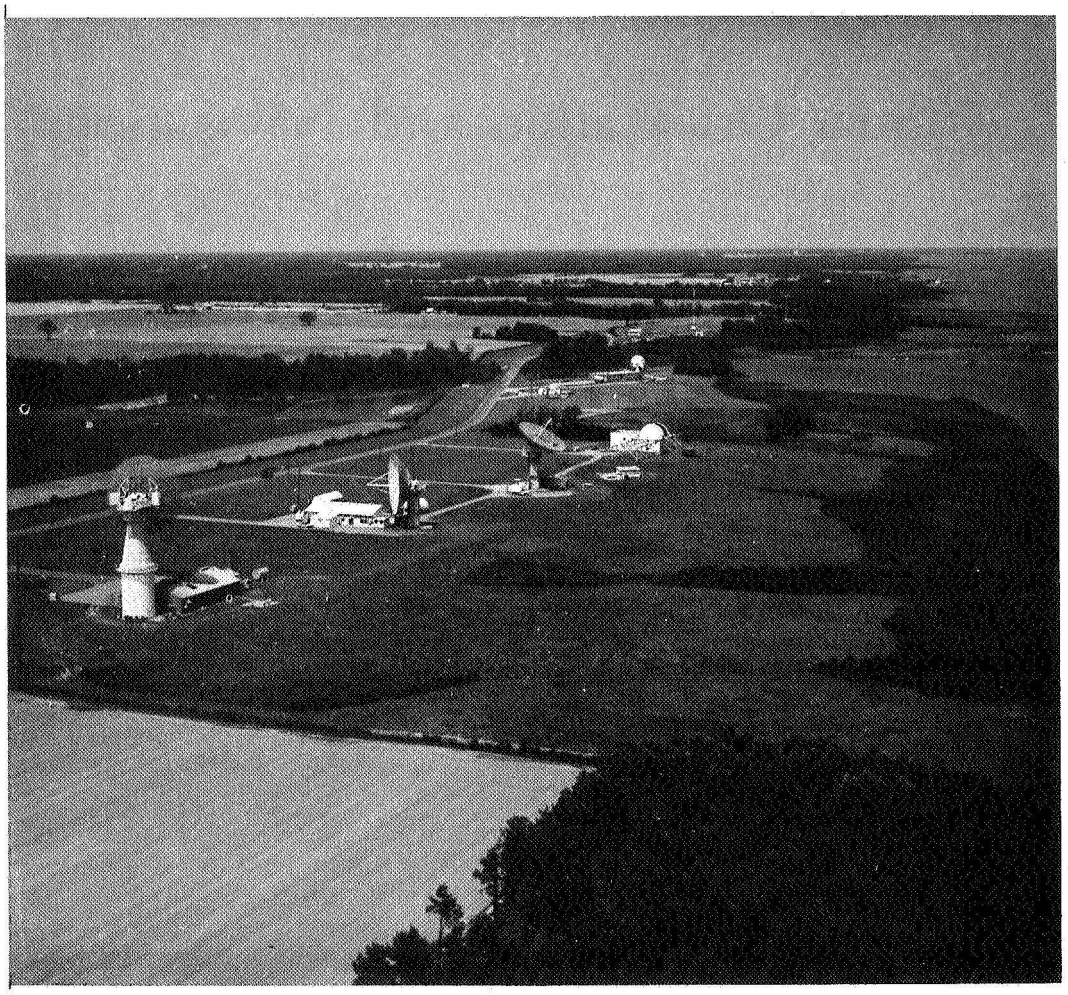


NATIONAL AERONAUTICS AND SPACE ADMINISTRATION

Animal Orientation and Navigation



Site of the radar bird tracking demonstration during the symposium at Wallops Station, Wallops Island, Virginia

NASA SP–262

ANIMAL ORIENTATION AND NAVIGATION

A symposium sponsored by the National Aeronautics and Space Administration, the Smithsonian Institution, and the American Institute of Biological Sciences and held at Wallops Station, Virginia, September 9–13, 1970.

Edited by
SIDNEY R. GALLER, KLAUS SCHMIDT-KOENIG,
GEORGE J. JACOBS, AND RICHARD E. BELLEVILLE

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Foreword

THE ORIGIN OF THIS VOLUME and the symposium proceedings it records can be traced to the deliberations of the National Academy of Sciences' Animal Orientation and Tracking Committee of the 1969 Space Biology Summer Study at Santa Cruz, California, whose members pointed to the potential role of satellites and recent bioengineering developments as a means of gaining information about the many questions of animal travel, particularly the mechanisms involved in long-distance navigational ability.

Coming several years since its predecessor conferences, at a time of a new popularization of ecology and a growing availability of advanced technology, the Wallops Station symposium reflected its temporal and geographic setting. The papers and discussions of this volume contrast the classical approaches to phenomena of ancient interest, the beginnings made in applying satellite technology, and the conceptual and methodological advances in experimental biology which have taken place in the past few years.

The range of species, sensory modalities, and methodologies provide the reader with a substantial sample of the developments in this field and with the basis for predicting, to some degree, its future course. Already apparent is the combining of field observations made under highly variable natural conditions with analytic, manipulative laboratory methods. A greater precision in the experimental questions now being posed is making their solution increasingly susceptible to neurophysiological and behavioral techniques for isolating the variables, both internal and environmental, which control this class of behavior.

Whether the mechanisms of orientation and navigation will yield to the current array of approaches addressed to specific questions or must await a more general understanding of brain function, there is little doubt that this symposium will have had a significant effect on the research to be reported whenever the participants in this field again assemble to assess their progress.

RICHARD E. BELLEVILLE
Bioscience Programs

SYMPOSIUM ON ANIMAL ORIENTATION AND NAVIGATION

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Acknowledgments

GRATEFUL ACKNOWLEDGMENT is made to the staff of the American Institute of Biological Sciences for their able and enthusiastic management of the administrative aspects of the symposium. A special tribute is due Mary-Frances Thompson, who served as the focal point of communication from the conception of the symposium through this final publication.

Recognition is also given to the Smithsonian Institution for its encouragement of the idea for holding a symposium of this nature. Financial support was provided by Bioscience Programs, Office of Space Science and Applications of the National Aeronautics and Space Administration, directed by Orr E. Reynolds. NASA Wallops Station, under the direction of Robert L. Krieger, served graciously as host for the meeting which was highlighted by a demonstration of its radar facilities actively engaged in tracking migrating birds.

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Keynote Address: The Long Research Mile to the First Small Step

DAVID D. ELLIOTT
National Aeronautics and Space Council
Executive Office of the President

I WOULD LIKE TO DISCUSS the important question of the application of your work on animal orientation and navigation. The most immediate and clear use of your findings and your techniques is in the areas of migratory patterns, animal conservation, and wildlife management. The application is less direct in the understanding of man, and particularly in attacking problems associated with man-in-space. So it is here that I would like to concentrate: on the study of animal behavior and its relation to manned space exploration.

Our success in landing men on the Moon is the direct consequence of an accelerating technology unparalleled in the history of mankind. The advances in materials, propellants, computers, communications, and navigation, occurring in less than a decade and a half and which have collectively resulted in the Apollo system, are nothing short of astounding. From my vantage as a physicist and a space scientist, I can review in my mind the sequence of these technological advances that derived from three decades of fundamental research in the physical and astrophysical sciences. The many debts that space technology owes to fundamental research on the broad front of the physical sciences are easily traceable, if not as publicly visible as I might wish.

However, the debts that manned spacecraft technology owes to the fundamental biological sciences are much less obvious, even to the biological scientist himself unless he was a direct participant in the pre-space age research programs in environmental physiology, animal orientation, and similar pursuits. In fact, a number of competent biologists have questioned the relationship of fundamental biological research and the technology of manned space flight. I emphasize that I am speaking of fundamental research, for the contributions to NASA's program in planetary quarantine and exobiology are acknowledged and easier to discern.

The difficulty in correctly relating biology to the manned program was made publicly evident in hearings before the House Committee on Science and Astronautics in November 1969. Those hearings revealed a sad lack of communication within the space

agency concerning the relevance of basic biological research to manned space flight.

What seems to have been overlooked, even among some distinguished practitioners of the biological sciences, is that one is misdirected in searching for a major impact on manned flight resulting from most of the basic biological research that has been conducted during the 1960's. This is because the biomedical data needed in the design of manned spacecraft for *short-term flights* were gained from basic biomedical research carried out and completed more than three decades ago! At most, the requirements for "new" biomedical information have been met by extensions and extrapolations of biological information that was published 20 to 30 years ago. In short, the fundamental difference between the physical sciences and the biological sciences, in their respective impact on the manned program (i.e., the manned program up until now) is a question of temporal ordering. The needed biology was done earlier.

But the manned program of the future is quite another matter. The years-long trips in Earth orbit or to the planets have not been researched to a point where we understand the problems, let alone the solutions. The physiological and psychological reactions to prolonged space flight are now only guessed at. And certainly before we undertake these trips, the fundamental work must be done. So with manned exploration of the planets waiting in the wings, the interest and attention of space explorers focuses on the preparatory work. Biological orientation and navigation, the subject of this symposium, promises to be an important element in this cosmic undertaking.

What is the history and what are the prospects of this application on your important research?

The field of animal orientation and navigation is quite new. If my sources of information are accurate, the initial impetus for the development of this field occurred in 1951, when a group of biological scientists, engaged in research on animal orientation, were brought together in a conference under the auspices of the Office of Naval Research (ONR) and the American Institute of Biological Sciences. During the first half of the 1950's, ONR was almost the exclusive sponsor of research in this field. A little later the Air Force Office of Scientific Research and, to a small extent, the National Science Foundation joined in support of this research. Now, approximately two decades since its formal recognition as a field, and a half dozen symposia and conferences later, NASA is serving as the principal American bearer of the torch.

And as NASA's interest in biological research is related to its fundamental mission of man-in-space, so the earlier sponsors, especially mission-oriented agencies, also had a purpose and a justification for supporting scientists in this particular quest for knowledge. The Navy and the Air Force were keenly interested in two aspects of orientation and navigation; first, to learn enough about the basic mechanisms by which animals are able to orient themselves in space and time, and thereby to help in the development of electronic analogues for target identification, selection, and navigation. Indeed, it is fair to say that the complex systems that animals use to navigate over great distances and to orient themselves, especially temporally, are marvels of micro-miniaturization and reliability, not yet duplicated electronically or mechanically.

The second interest was a more urgent and pragmatic one. The military's experience with high-altitude, high-speed aircraft, as

well as in sustained undersea submarine operations, convinced them that there were serious disorientations and biological "clock" problems. And these problems would have to be solved in order to protect pilots against psycho-physiological disturbances associated with trans-longitudinal flights encompassing several time zones and taking place over short periods of time. In the case of sustained undersea operations, failure to reproduce conditions for maintaining normal biological cycles produced fatigue and disorientation. The phenomenological basis for these problems is today well recognized, but such was not the case as recently as a decade ago. Today, even though we still do not understand the underlying mechanisms, we do know enough about the effects of disruptions of biological clocks and circadian rhythms to warrant the development of a set of admittedly empirical but relatively effective protective measures.

Fundamental scientific interests in this extraordinary field of the study of orientation, navigation, and the biological clock have not really changed in any dramatic fashion in the last decade. Scientists, however, are concentrating more on elucidating the underlying mechanisms and less on the phenomenological aspects of the problems. What have changed are that certain new research tools have become available to you and that space technologists have been added to that body who will use and apply your findings.

In the category of new tools, the use of satellites to track tagged animals in otherwise inaccessible areas, such as the pioneering study of elk from NIMBUS–B, is a new and imaginative innovation. This method will and should be exploited to learn more of migration and behavior.

In the matter of application, it is man-in-space that is your new user. Understanding of the subtle, psycho-physiological and biophysical mechanisms that drive all levels of biological organization is a requirement in designing functional man-machine systems for extended voyages in outer space. But to see that this understanding is correctly incorporated in these designs is, I believe, a special duty of yours. This is not a duty of your own choosing, and it is one that is outside the scientist's traditional role. The great majority of scientists, who do research where their interests and talents lie, present their results freely and openly and then stand aside while technologists apply their findings, when possible, to the problems of man and his environment. Great things have happened under this arrangement. But will it suffice for your work? I question that it will. That traditional development has the drawback of slowness and also often involves incomplete or poor communication. With the space age, and particularly in the space program itself, time and developments move at orbital speeds. The systems for planetary exploration are now in men's minds or are sketches on paper. If these systems are to account properly for man's biological peculiarities and uniqueness, it is imperative that your work and your ideas be fed into the plans at their formative stage. Hence the reason for my feeling of urgency and why I believe you have a special duty. The responsibility falls to you not only to do your own research, but it is imperative that you assist and direct the application of your results to the manned space systems that will soon develop. For if you do not provide this guidance and help, the manned systems will get away from us, and end up being developed purely empirically with attendant loss of time, money, effort, and possibly lives.

Perhaps we need a kind of expeditor or somebody akin to the interlocutor in the old-

fashioned minstrel show who can bridge the gap and catalyze the dialogues between the technologists and the biologists that will be so essential in developing the space vehicles of the future. It may well turn out that our human endeavors in space will depend more on the incorporation of knowledge gained from fundamental research on organisms, up to and including man, than on advances in physical technology.

We have a long road ahead of us in learning enough about the fundamental phenomena and mechanisms that initiate and drive living systems. And then we must insure that the marvelous vehicles to be developed will be able to house and maintain functional man for the indefinitely long periods of time needed to explore the outer limits of our solar system.

In closing, permit me to hope that one of the essential by-products of this symposium will be the recognition of the need to develop an effective dialogue from biologist to engineer, in addition to the more traditional, but highly desirable, transfer of fundamental knowledge from one biologist to another.

SESSION I

Techniques

Chairman, JOHN H. BUSSER

Use of the Doppler Technique to Track Free-Roaming Animals from Satellites

JAMES C. MAXWELL
Smithsonian Institution

RADIOTELEMETRY has been developed over the years as a useful tool for the investigation of animals under natural field conditions. However, our present ground radiotelemetry has limited tracking range and the investigator must move with the animal to stay within range. A ground tracking range of 16 km is typical. The use of aircraft increases the tracking range to around 160 km but involves the expense and limitations imposed by the aircraft.

These range limitations of ground radiotelemetry will probably not be overcome with better technology. Fundamentally we are faced with a power-limited transmitter on the animal and a poor communication path made up of a conductive earth boundary, with hills, forests, and water to attenuate the transmitted wave. It takes less power to transmit a television picture from the Moon to Earth than to send the same picture 3200 km along the surface of the Earth. We can expect that our present ground-based tracking range of 16 to 160 km is representative of our technological capability and that this range will not soon significantly improve.

Satellites can be used to overcome this range limitation by providing a line-of-sight (LOS) communication path with the animal. The transmitted wave then suffers only the space loss and does not have to bend with the Earth's curvature or pass through interfering forests.

A satellite in a circular polar orbit of 800 km comes within LOS of any point on the surface of the Earth every 24 hr. At the equator, the satellite passes within LOS once every 12 hr; and at the poles, every 90 min. A satellite in a polar orbit "covers" the Earth. This is the reason the Nimbus satellites are placed in a polar orbit enabling them to "see" the weather conditions anywhere on the globe.

Similarly, an animal transmitter can communicate with a satellite in a polar orbit (such as Nimbus) at least once a day from the equator and every 90 min from the poles. After the investigator has mounted the package on an animal, a satellite with ground data-reduction facilities will produce a computer printout giving the animal's location and physiological data.

DESIRABLE CHARACTERISTICS OF AN ANIMAL-MONITORING SATELLITE SYSTEM

For a satellite system to find widespread application in wildlife research, it must be designed with the single goal of producing lightweight, low-cost animal packages. Requirements for accuracy in location, physiological data, and animal-package lifetime are secondary considerations. Figure 1 summarizes radiotelemetry animal experiments and the package weights.

A large variety of animals will be instrumented, and they will be capable of transmitting widely different amounts of radio-frequency power. Elephants can carry a heavy package capable of transmitting several watts. Large birds can transmit only 10^{-3} W for any reasonable tracking period.

A reasonable engineering compromise between the satellite capability, the limitation on animal-package output power, and the level of engineering difficulty (cost) suggests the following requirements for an animal-tracking satellite system.

(1) The satellite must be capable of monitoring up to several hundred animals at one time.

(2) The animal's position P must be determined to $\pm$ 1 km $< P <$ $\pm$ 40 km. Most experiments in long-range, continental animal tracking would be satisfied with $P \leq \pm$ 10 km.

(3) The animal must communicate with the satellite at least once every few days. When battery power is limited, an animal transmission to the satellite once a week can provide useful tracking information.

(4) In addition to the animal's position, the satellite must be capable of collecting at least five separate physiological parameters. The physiological parameters should be measured to within a $\pm$ 10 percent error of the physiological transducer output.

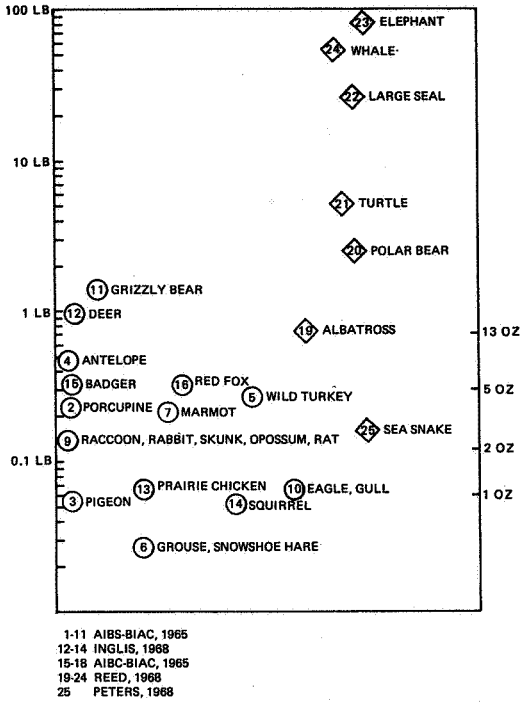

FIGURE. 1 Estimated weights animals can carry. The circle denotes experiments that have been done; weights include transmitter and batteries, but not harness. The diamond denotes rough estimates of what animals can carry.

(5) The weight W of the complete animal package must be as little as possible, 25 g $< W <$ 2 kg. This requires the satellite receiver to process different signal strengths transmitted from the animal package on Earth. Typically the transmitted power P will be 10^{-3} W $< P <$ 10 W.

(6) As a design goal, the animal package should cost only several hundred dollars.

(7) The lifetime of the animal package must be at least 3 months. Lifetimes of 1 yr or more are needed for long-term studies.

(8) The animal package should be simple and require no field adjustments.

RELEVANT EXISTING SATELLITE SYSTEMS FOR ANIMAL TRACKING

Three satellite systems currently either under development or being used by NASA satisfy some of these requirements.

(1) FR–2 (EOLE) a joint France-U.S. experiment;

(2) The Interrogation Recording and Location System (IRLS);

(3) The Omega Position Location Equipment (OPLE).

These systems determine the position of and collect physiological data on ground packages (table 1).

In the EOLE system, platform location is determined from the simultaneous measurement of satellite-platform range and indirect measurement of the angle between the propagation path and the satellite velocity vector. To accomplish this, the satellite broadcasts tone bursts, which are received by the package, translated in frequency, and retransmitted to the satellite. The satellite then measures the frequency difference (doppler) and time difference (range) between the transmitted and the returned signals. It stores in its memory these values, along with any transducer data included in the returned signal, for later retrieval by a ground station. The estimated uncertainty of the locations derived from these measurements is ± 2 km.

IRLS is similar in operation except that IRLS determines only satellite-to-package range by measuring the satellite-package radio-propagation delay. The uncertainty of the location derived from the measurement is ± 2 km.

In the OPLE project, the package receives VLF transmissions from the U.S. Navy's ground-based OMEGA navigation network, converts the signals to VHF frequencies, and transmits them to an OPLE Control Center via a synchronous-satellite transponder. The platform location is determined at the control center from the isophase contour lines generated by the phase difference between signals from the three OMEGA

TABLE 1.—*Summary of Characteristics of Present Satellite Tracking Systems*

	NASA systems		
	EOLE	IRLS	OPLE
Satellite:			
Designation	FR–2	Nimbus	ATS–3
Launch date	Dec. 1969 or July 1970	May 1969	Feb. 1968
Inclination	65°	90°	0°
Package required:			
Weight	4 lb	10 lb	44 lb
Cost	$10 000 each	$10 000 each	$25 000 each
Transmission power	4 W	5 W	35 W
Standby power	0.1 W	0.1 W	1.1 W
Transmission frequency	400 MHz	465 MHz	149 MHz
Reception frequency	460 MHz	400 MHz	136 MHz+VHF
Interrogation time	2×600 msec	2×3 sec	198 sec
Coverage of Earth's surface	Blind areas near poles	Complete	Part of western hemisphere
Accuracy	±2 km	±2 km	±500 m (potential)

transmitters. The potential uncertainty of OPLE location measurements is quoted as ± 500 m (800 km). The weight (20 kg) and large size (due to the necessarily large VLF antenna) of the present OPLE package eliminate it almost immediately from serious consideration as an animal package.

These three systems have two features in common that prevent them from being universally adaptable to tracking animals. The packages are too heavy to be carried by most animals and, because they are electronically complex, weight reduction is difficult. The cost of the packages prohibits any systematic use of these satellite systems, and again their complexity rules out any possible reduction in cost to approximately $100 per package.

THE DOPPLER TECHNIQUE: A GOOD SYSTEM FOR SATELLITE ANIMAL TRACKING

The doppler satellite-tracking technique is ideally suited for satellite monitoring of animals. No other satellite technique offers the same theoretical advantages of narrow bandwidth and has the same general system flexibility to meet the varied requirements of animal tracking.

Simplified Explanation of the Doppler Technique

Consider an observer O moving along a known path C with velocity V, and a transmitter located at L. The observer is located at t_1, $t_2 \cdots t_n$ as he moves along path C. The transmitter is radiating a single frequency f_0 (fig. 2).

The observer will measure a received frequency f_r, modified from f_0 by the observer's velocity. This is the well-known doppler effect and is readily observed by listening to the horn of a passing automobile. The measured frequency f_r at each t_n is shown in figure 3.

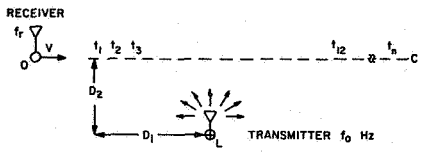

FIGURE 2. A receiver moving along *C*, with *L* fixed, measures the Doppler curve of figure 3.

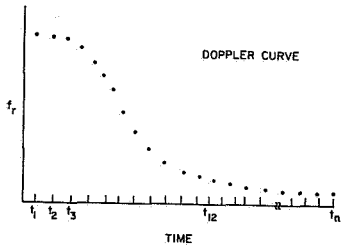

FIGURE 3. Doppler curve.

If we are given only the doppler curve shape of figure 3 and path C — that is, if we know the location of the observer at t_1, $t_2 \cdots t_n$ — we can find the location of the transmitter L relative to C. For example, assume we can solve for D_1 and D_2 from the doppler curve and fix the transmitter relative to t_1. If at t_1 we are located 6 mi north (from some reference) and $D_1 = 1$ mile, $D_2 = \frac{1}{2}$ mile, then the transmitter is 7 miles north and 0.5 mile east or west. We obtain an east-or-west solution since the doppler curve is identical for both sides of path C; therefore, we always have two locations. One of the locations must be ruled out from some other knowledge. This is usually done from information on the earlier position of the transmitter, or its possible range of travel, or some physical characteristic of the location. For example, the transmitter is not east of C because there is a large lake there.

The problem is reversible. That is, we can interchange the transmitter and receiver and from L solve for path C. Indeed, an

early method of measuring satellite orbits consisted of measuring the doppler shift received on the ground from the satellite transmitter moving with velocity V. This interdependency of transmitter location and measured doppler curve formed the basis for the Navy "Transit" satellite navigation system.

The Relationship Between the Doppler-Effect Curve Shape and the Transmitter Location

Figure 4 is an inverted doppler curve measured for 200 seconds of the Explorer 1 satellite pass. The received frequency f_r was measured at 1-second intervals, bad measurements were rejected, and the resultant curve was plotted.

As an aid in understanding the position/doppler relationship, consider figure 4 and the following steps:

(1) We connect the points with a smooth curve.

(2) We find the inflection point on the doppler curve and mark its time T_i. At T_i, the satellite must be at right angles to the transmitter. (Figure 5 presents the geometry of the problem.)

(3) The satellite orbit is known. We know the location of the transmitter plane from step 2.

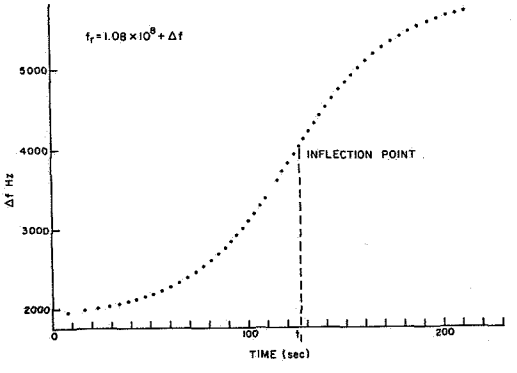

FIGURE 4. Doppler curve measured with the Explorer 1 satellite (1958).

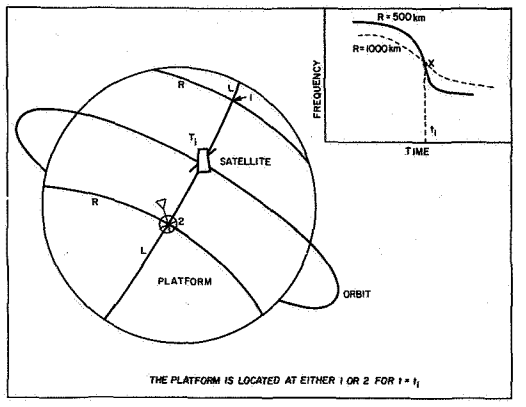

FIGURE 5. Doppler curve/platform location geometry.

(4) The transmitter is on the surface of the Earth. Then the transmitter must lie on the line L formed by the intersection of the plane and the surface of the Earth.

(5) The overall shape of the doppler curve gives the range R to the transmitter. For example, $R = 500$ and 1000 km is shown in figure 5 to illustrate how the Doppler shape changes with range. A computer is usually employed to fit the known Doppler curve for each range case. The range curve that produces the minimum errors is the range R to the transmitter. As a rough indication of range,

$$R = \frac{f_t f_r^2}{c(df_r/dt)}$$

where

f_t = transmitted frequency (Hz),
f_r = received frequency (Hz),
c = speed of light (3×10^8 m/sec),
df_r/dt = slope of doppler curve at T_i (Hz/sec).

(6) The animal transmitter is located at positions 1 or 2. Knowledge of a previous position will fix either 1 or 2 since they will be located hundreds of kilometers apart.

Measurement errors affect the location accuracy. A 1-sec error in locating the doppler inflection point moves the plane of the transmitter

7.6 km/sec (satellite velocity) $\times$ 1 sec = 7.6 km error.

From figure 4, the slope

$$\frac{\Delta f_r}{\Delta t} \doteq \frac{2000 \text{ Hz}}{67 \text{ sec}} \doteq 30 \text{ Hz/sec} \qquad (t = T_i)$$

or

30 Hz = 7.6 km error, $f_0 = 108$ MHz

3×10^{-7} frequency error = 7.6 km location error.

We are interested in the frequency stability for the 10 minutes while the satellite is in view:

$$\frac{3 \times 10^{-7} \text{ Hz}}{10 \text{ min}} \doteq 2 \times 10^{-6} \text{ Hz/hr}$$

and

2×10^{-6} Hz/hr crystal stability = 7.6 km location error.

A crystal-controlled oscillator with no oven but with 2 inches of thermal insulation to hold the crystal and circuits to within 0.1° C for 10 minutes will provide sufficient frequency stability to limit our position error to $< \pm 3$ km.

Very small packages, such as for birds, will not be able to insulate fully the crystal unit and will therefore have a larger positional error. However, the positional error should remain less than ± 30 km except when very large changes in the ambient temperature occur during the 10-minute satellite pass.

Choices of Animal Package for Use with the Doppler Technique

A lightweight Doppler transmitter providing only position information is diagrammed in figure 6. The crystal oscillator will operate at the frequency assigned for the animal. The timer can be used to turn the transmitter on and off and thus conserve battery power, which will extend the transmitter lifetime for a given weight of batteries, thus providing the ultimate in lightweight transmitters for small animals. Figure 7 shows a second type of transmitter, in which a timer is used to

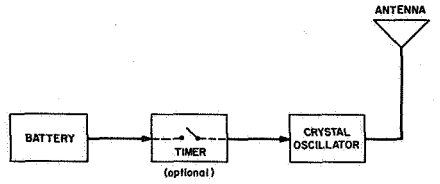

FIGURE 6. The lightweight (position only) animal package.

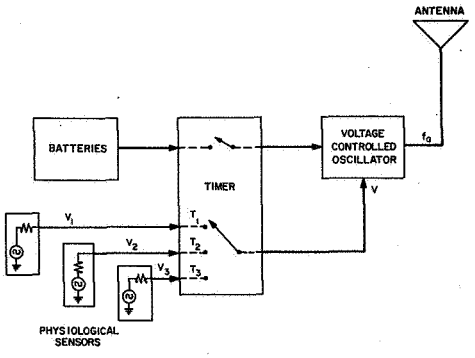

FIGURE 7. Position and physiological-data animal package.

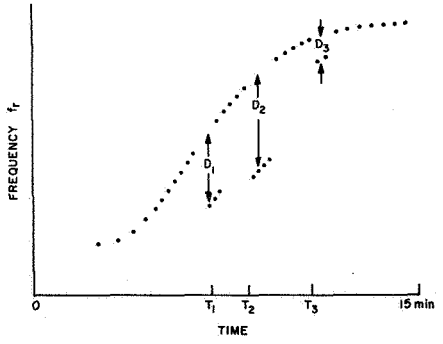

FIGURE 8. Doppler curve with physiological data, D_1, D_2, and D_3.

commutate physiological data into a voltage-controlled oscillator. This package will also give the animal's position.

The physiological data will appear on the Doppler curve as frequency deviations. Figure 8 is an example of such an output. We identify the channels by their time separations and order T_1, T_2, T_3, $T_2 - T_1 = 1$ min, $T_3 - T_2 = 2$ min. The amount of frequency deviation D is proportional to the physiological-sensor voltage output v. Then, from the Doppler curve we measure D_1, D_2, and D_3 and obtain v_1, v_2, and v_3. The f_r data points during the time that physiological data are transmitted are ignored when determining location.

We can estimate some sizes and weights for the animal packages for the doppler technique.

At the output of the satellite receiver tracking filters, having a bandwidth B, the S/N (signal-to-noise ratio) is given by

$$S/N = \frac{\lambda^2 P_T D_T D_R E_R I L}{(4\pi R)^2 k T_{eq} B}$$

where k is Boltzmann's constant and the other quantities have the values noted in table 2. Then, with $R = 3 \times 10^6$ m, $T_{eq} = 1200$ K, $P_T = 225$ mW, $B = 50$ Hz, $\lambda = 0.3$ m,

$$S/N = 8.9 \text{ dB}.$$

For birds and other small animals, we must operate at the frequencies available from crystal units. This restricts our maximum frequency to $f_0 \leq 100$ MHz, $\lambda \geq 3$ m. For larger animals, where there is room for frequency-multiplication stages, we can choose f_0 at our convenience. A small λ enables us to work with small antennas. A $\lambda = 0.1$ m produces an antenna with circuit polarization that occupies less than $4 \times 4 \times 2$ inches. Table 3 summarizes the design choices and the resultant animal packages.

Satellite Requirements for the Doppler Technique

As a reasonable design choice, the satellite system must receive and process 10 separate

TABLE 2.—*Values of Quantities Used in Determining* S/N *Limits*

Symbol	Quantity	Value	Remarks
λ	Operating wavelength	$0.1 < \lambda < 4$ m	Ionosphere restricts $\lambda < 4$, Electronics restricts $\lambda > 0.1$
P_T	Radiated power	$10^{-3} < P_T < 1$ W	Power level compatible with small animal packages
D_T, D_R	Directivity of transmitting and receiving antenna	1	Isotropic antennas
E_R	Receiving antenna efficiency	80%	Some loss in antenna-to-receiver cable
I	Ionospheric attenuation	1	$\lambda < 6$ m
L	Polarization loss	½	Linear antenna polarization assumed
R	Transmitter-to-satellite range	$R < 3 \times 10^6$ m	Satellite elevation $\phi = 10°$
B	Bandwidth of satellite receiver filter	5 Hz $< B <$ 50 Hz	$\lambda = 3$ m
T_{eq}	Satellite-receiver equivalent-noise temperature	$1200 < T_{eq} < 7900$ K	Satellite-receiver noise figure $F = 6$ dB

TABLE 3.—*Animal Packages for the Doppler Technique*

Animal (attachment)	Electrical power	Total animal package weight (~80% batteries)		Lifetime (days)	Rate of locating $1/T$	Remarks
Eagle	Hg battery	1.2 oz	*	31	>1/day	$P_T=10^{-3}$ W $B=0.5$ Hz, $f_0=100$ MHz $E=20\%$
Albatross	$50\ \frac{W\text{-}H}{\text{lb}}$	1.7 oz	t_1	217	1/week	
		3.4 oz	*	88	>1/day	No physiological data
Caribou	Ag-Cd battery and solar cells	1.4 lb	t_2	136 952	1/day 1/week	$P_T=225\times10^{-3}$ W
Polar bear (collars)	$30\ \frac{W\text{-}H}{\text{lb}}$	8.5 lb	t_1	70	1/week	$B=50$ Hz, $f_0=1$ GHz $E=25\%$
		8.5 lb	t_2	1000	1/day	With physiological data
Sea turtle	Ni-Cd battery	20 lb	t_2	925	1/day	
Whale (marine float)	$13\ \frac{W\text{-}H}{\text{lb}}$	(600 in.^{3})		6475	1/week	
Elephant (harness)	Ni-Cd battery and solar cells	20 lb	t_2	Indefinite	1/day	

*=No timer
t_1=With timer set for "on" for 24 hr, "off" for 1 week
t_2=With timer set synchronous with the satellite pass, "on" for 15 min, "off" for T
P_T=Transmitted power (W)
B=Required satellite receiver (tracking filter) bandwidth (Hz)
f_0=Transmitter frequency (Hz)
E=Efficiency of the animal package electronics

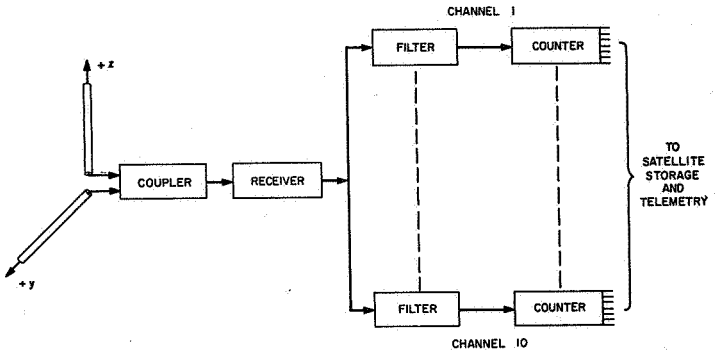

FIGURE 9. Block diagram of the equipment required in the satellite.

frequencies from the ground transmitters. The 10 frequencies will enable the satellite to track several hundred animals a day, although only 10 animals can be tracked in a small area that is within a single LOS of the satellite.

Figure 9 is a block diagram of the satellite receiving and processing system. The tracking filters have bandwidths of several hertz and are used to extract the transmission frequency of the animal package from the background electronic receiver noise. The counters measure and present the received frequency to the satellite telemetry system in digital form. Later the satellite will send the measured frequency to the ground station for analysis. The output of these counters is the frequency points f_r that make up the doppler curve.

The satellite telemetry must process a data rate R of 4 bits/sec $< R <$ 20 bits/sec. The data processor consists of 100 integrated circuits (flat packs). The tracking filters could be made up of the Signetics NE 561B phase-locked-loop integrated circuits. The satellite receiver must be a wideband UHF type. The 10 frequency bands will be widely separated in the UHF range and may require two separate mixing operations. The satellite antenna can be a crossed dipole configuration. Four arms, each 10 inches long, extending from the body of the satellite will satisfy the antenna-gain requirements. The following Doppler equipment characteristics are required in the satellite:

(1) Size: 66 in^3
(2) Weight: 1.5 lb
(3) Power consumed: 4.7 W
(4) Data rate to telemetry: 4 bits/sec $< R <$ 20 bits/sec

CONCLUSION

The Doppler technique is ideally suited for use in tracking animals from satellites. The narrow bandwidth inherent in the technique provides the electronic design flexibility needed in animal work. It also will result in the smallest, lightest, and simplest animal package possible. No other radio technique will offer a better animal package. In addition, the narrow bandwidth of the satellite receiver is much less sensitive to electrical interference when compared to more conventional wideband receiving systems.

I intend to continue the Smithsonian effort to help NASA provide for this satellite animal-tracking capability. We proposed this Doppler technique to NASA early in 1968, and I am encouraged by NASA's support

for my design efforts in these years of shrinking budgets. We hope to make a rather simple test of this Doppler technique in early 1971 using Nimbus IV. I expect to see a satellite Doppler capability by 1974 that will enable investigators throughout the world to mount $100 transmitters on animals and obtain, in the mails, the daily location and condition of the animal.

DISCUSSION

GRIFFIN: What kind of an antenna must the animal carry for this apparatus to work effectively?

MAXWELL: For small animals a short piece of wire several inches long may be used. Since it is necessary to radiate a milliwatt (at 100 MHz, this is a fraction of a wave length) the efficiency will go down to 10 to 20 percent, a very low efficiency system. For larger animals a larger dipole will be used. At 1 GHz the antenna is four inches by four inches by three inches.

WILLIAMS: There is one problem to be considered if this system is used on birds. While the temperature stability can be solved by simply putting the unit underneath the feathers, the unit components are affected, particularly by antenna loading, by the wing beats of the bird. We get a 5-kHz change just in the motions of the bird; if the bird is actually touching the antenna you get many many times that.

MAXWELL: Your crystal oscillator is overly frequency sensitive to the varying antenna driving point impedence. The driving point impedance of the antenna changes with the relative position of the wings to the antenna.

WILLIAMS: How are you going to get around the frequency shift unless you have shielding?

MAXWELL: It may be necessary to add an active stage to buffer the crystal from the antenna. Certainly the frequency "pulling" of the crystal can be held to a few hertz.

WILLIAMS: The whole system is based on a very high degree of frequency stability. A very small transmitter near a small electromagnetic generator (the bird) makes it difficult to get frequency stability. Some thought must be given to this problem.

MACKAY: If the crystal of an oscillator is shaken up and down, as by the movements of a bird, some crystals will show a shift in frequency that is of the order of the required stability. Some crystals used in a fundamental mode will show less stability than an overtone crystal.

A separate output stage on the transmitter seems required, and some of these, as well as some frequency multipliers, are significantly less affected by changes in the surroundings than others. Light electrical shielding need not interfere with the bird. Perhaps a greater problem is reliable automatic release of an attachment to the bird that does not interfere with his normal activities. Some of the biological problems seem more difficult than the electrical ones.

WALCOTT: I would just like to emphasize the last problem. In designing these transmitter packages, it is absolutely crucial to work on both the biological as well as the engineering problems.

BUSSER: The very existence of the AIBS Bio-Instrumentation Advisory Council as a go-between or the catalyst in this area, shows that both sides are certainly not ignoring this problem of communication. It is very real.

GRIFFIN: How long a monitoring period is available?

MAXWELL: The satellite is in view for about 10 min every 12 hr. You could use most of this 10-minute period to monitor a transducer or a data storage device. However, you are limited to the 10 min if you wish real-time information.

GRIFFIN: Could you, for instance, use the closest part of the curve for position information while transmitting physiological data before and after, when it is still within range?

MAXWELL: No. The trouble is, you never know when the satellite is at right angles. You don't know when you are at the center of the Doppler curve.

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Long-Range Radio Tracking of Sea Turtles and Polar Bear—Instrumentation and Preliminary Results[1]

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and
The University of Arizona

THIS PAPER describes instrumentation developed for studies of path behavior of the green sea turtle (*Chelonia mydas*) and migration movement of polar bear (*Thalarctos maritimus*) and gives preliminary results bearing on navigation ability in these species. Both species operate in difficult environments, and the problems faced in the design of electronic instrumentation for these studies are not completely specified at this time. However, the critical factors yet to be understood are primarily related to the behavior of instrumented animals.

Both telemetry systems are intended to provide tracking data at ranges of approximately 185 km (100 nm). The application of waveguide techniques to UHF antennas (ref. 1) has resulted in an efficient omnidirectional antenna approximately 2.5 cm in height for use with polar bear. A desirable feature is the packaging that allows all electronic components to be embedded compactly in plastic for both mechanical protection and immersion in salt water. The marine turtle instrumentation incorporates telemetry of directional and velocity data at periodic intervals. This feature frees the experiments from the need to maintain bearing data from known geographic locations to reconstruct movement patterns of instrumented turtles at sea. This feature is particularly valuable for studies involving the testing of navigation ability under experimental constraints.

The data obtained with these experimental techniques are included in this report, first to illustrate the technique and, second to provide initial preliminary results bearing on animal navigation.

TURTLE INSTRUMENTATION

Marine turtle radio tracking experiments have been underway for about 3 years. A

[1] Studies of the green sea turtle are in collaboration with Archie Carr, University of Florida, and the polar bear studies are in collaboration with Jack W. Lentfer, Alaska Department of Fish and Game. Donald L. Brumbaugh contributed electronic instrumentation design, and Dale E. Hall mechanical design. Both are members of the Sensory Systems Laboratory.

This work has been supported by NASA Grant NGR-03-041-001, ONR Contract Nonr-4315(00), and by the Alaska Department of Fish and Game Federal Aid in Wildlife Restoration Project W-17-2.

radio frequency was selected in the HF band allocated for unattended buoy operation by the Federal Communications Commission. Narrowband, low-power operation at 8 MHZ was found to be satisfactory for ground or sky wave propagation over sea water at ranges on the order of 185 km (100 nm). Reception is available periodically at increased ranges, depending upon ionospheric conditions. In the summer of 1967 a tracking experiment was initiated at Tortuguero, Costa Rica, using a periodically transmitted cw signal and dual phase locked receivers (ref. 2). Two vertical antennas spaced one half wavelength apart provided an azimuth track of the float position from the launching point of the turtle. After approximately 1 hour and 20 minutes, sharks were observed near the float and the signal disappeared. The experiment and subsequent discussion provided two significant conclusions: (1) Telemetry equipment would have to withstand shark attack, and (2) path behavior (that is, periodic transmission of turtle heading and swimming speed from the float) would be more valuable than geographic position in understanding the factors that provide orientation to a migrating turtle.

During the later part of the nesting season in October 1968, a second attempt was made to track a turtle at Tortuguero. The instrumentation contained the following:

(1) A float consisting of a sealed aluminum pipe 12.7 cm in diameter, 2 meters in length, balanced with a keel to support a vertical whip antenna.

(2) A wand type velocity probe whose deflection due to relative movement between the float and the water was sensed with a linear differential transformer.

(3) A spinning magnetometer consisting of a moving coil for sensing the earth's magnetic field for directional bearings.

(4) Timing, logic and coding to key a transmitter with pulse-time cw modulation at 20-minute intervals.

(5) An 8 MHZ tranmitter providing approximately 1-watt input to a loaded vertical whip antenna. A long-life battery pack was provided.

At 1020 hours on September 29, 1968, the float was attached to a mature female turtle and launched. The line between the turtle and the instrumentation float was 21 meters in length—considered to be sufficient for a float to remain at the surface during the migration from the nesting beach to one of the various feeding grounds located throughout the Caribbean. A piece of iron wire was used in the attachment to provide an automatic release mechanism for the turtle after several weeks.

Tracking data were obtained during the subsequent 4 days and are summarized as follows:

For the first 6 hours the turtle headed generally away from the shoreline and then turned north in the afternoon. Heading and swimming speed data indicated that she turned toward shore during the night. The heading suggested that the current at the mouth of the Tortuguero River and along the coast was responsible for the apparent velocity and direction data recorded. The currents along this coast are induced as a backwash of the Gulf Stream, and it was necessary to assume an average rate of water movement of 0.496 km (0.3 mile) per hour to the southeast along the shoreline to provide correlation between visual sightings of the float and integrated movement vectors from telemetered data.

A visual determination of the float position was made at 0608 hours on the morning of the second day, September 30. The turtle continued a northwesterly heading until 0806 hours. The investigators approached the instrument float in a small boat at 1026 hours

and as soon as it was touched the turtle sounded, taking the float under the surface at a steep angle. It resurfaced in about 15 meters, and no further attempt was made to physically contact the float. In the afternoon at 1647 hours, signals were interrupted by radio interference and radio contact was not reestablished until 0555 hours the morning of the third day. During the night the interference decreased and signals from the float were still not available. There is considerable likelihood that the turtle submerged and rested during the night at a depth sufficient to take the instruments below the surface.

Bearing and velocity data resumed at 0555 hours and continued throughout the third day and night. There is a suggestion that turtle swimming inactivity in the early morning hours on the morning of the fourth day can be inferred from the bearing data.

Bearing and velocity data were received until 1518 hours, October 2, the fourth day after release. At that time the transmitter signal was heard continually without data modulation for the following 3 days. This indicated a malfunction in the programming circuits that would have caused a rapid dissipation of battery power. The instrument float was recovered on the beach October 14, 16.7 km north of the release point.

The following information was considered pertinent from this work with regard to the design of future experiments:

(1) The heading data gave a reasonable picture of path behavior with regard to navigation ability. Headings were generally consistent and inferred that a single prevailing direction was maintained. The absence of a dispersion or randomness to heading data tends to weaken an hypothesis dependent on sampling for olfactory cues. On the other hand, the importance of the abundant clues for guidance available from the coastline in terms of wave noise, salinity changes, water depth and others would make it quite possible for the turtle to maintain a reasonably constant heading parallel to the coast.

(2) The weakness of the data lies in that it provided no reference to geography once the float was not visible. The magnitude of the Gulf Stream countercurrent was unsuspected at inception of the experiment. Velocity data were unreliable for two reasons: (a) the vertical movement of the tethered float in waves was found to create an error in apparent speed, and while the error was small compared to the swimming velocity, it was cumulative; and (b) the strong currents in the waters near the coast tended to override the velocity information sensed at the float. In one case the velocity data showed the turtle proceeding to the north when, in fact, the float was observed being carried to the south. This discrepancy was particularly evident at night when the turtle appeared to rest.

The data lost due to radio interference on the short wave frequencies amounted to 5.5 percent of the data transmitted, if we assume that the float was submerged the second night after release. Interference occurred primarily at night when the conditions for skip or ionospheric propagation modes occur. The following conclusions were made:

(1) Future experiments using telemetry would require a direction-finding system in addition to vector movement data, particularly when studies occurred close to land.

(2) The velocity sensor based on deflection of a probe should be abandoned in favor of an ultrasonic system.

(3) The float would have to be submergible.

Preparations for the third attempt to track *Chelonia* during its migration (this time at Ascension Island in the mid-Atlantic) were begun soon after the work at Tortuguero. Design concepts included:

(1) A velocity sensor based on detection

of Doppler shift by ultrasound. Ultrasonic energy is beamed into the water and the backscattered energy is detected and analyzed. Relative movement between the sensor and the water is detected as a frequency shift between the generated energy and the scattered energy. The unit was tested extensively and found to operate in the Gulf of California and in several lakes. It was noted, however, that pure water did not provide sufficient scattering to give a detectable signal. A few particles from 1 to 10 microns in cross section did provide an adequate signal.

(2) Loop antennas were designed for direction finding bearing accuracies of $\pm 1/4°$ at ranges of 18.5 km (10 nm), and $\pm 5°$ at ranges of 185 km (100 nm).

(3) Transmissions occurred at 10- rather than 20-min intervals.

(4) All electronic subassemblies were hermetically sealed in aluminum canisters designed to withstand submersion.

(5) Four floats were prepared for the Ascension Island tests. All were to transmit on the same frequency and if used simultaneously, they were to be distinguished by the time of transmission. The clock mechanism was electromechanical so that reference to standard time could be maintained.

When the instrumented floats arrived at Ascension Island they were found to have been damaged in shipment. All of the compass shafts were broken, indicating that the floats had sustained high impact forces. The instruments were repaired or redesigned as well as possible, calibrated, and tested extensively.

On April 7, 1969, an instrumented turtle weighing some 300 kg was transported 187 km (101 nm) north-northwest of Ascension Island and released. Data transmissions were received for the next 2 hours and then abruptly terminated. Heading data were remarkably constant and indicated a bearing almost directly towards Ascension Island; velocity data were not present in the transmission. We have assumed that the lack of particulate matter in the ocean reduced the backscattered energy below detectable limits.

There were no clues as to the cause of cessation of signals from the float. The float was not recovered at Ascension Island and no facilities were available to inspect the area from which the last transmission was made. Conjecture runs as follows:

(1) The turtle submerged to unexpected depths. No information is available as to the maximum diving capability of this species.

(2) There is a small but finite possibility of physical interference with the experiment.

(3) Failure of electronic components could have occurred.

(4) Large sharks are frequently observed in the water adjacent to the island, and shark interference is possible.

Tests were continued in the summer of 1970 at Tortuguero, Costa Rica. The equipment used is basically that given in the Appendix, with the following exceptions:

(1) The velocity indicator is a commercially available "paddlewheel" type[2]. The paddlewheel contains small magnets that provide four impulses per revolution. These impulses are stored in a capacitor memory and translated to a pulse code in such a way that velocity is given by counting the number of transmitted pulses.

(2) While the spinning coil magnetometer was reliable in use, it was desirable to eliminate the mechanical problems of the moving coil, together with the power consumption of a small motor. A miniature two-axis fluxgate magnetometer designed and described by C. J. Pellerin and M. H. Acuna (ref. 3) was employed.

[2] Signet Scientific Co., Burbank, California, "Knotmeter."

(3) The float was reduced in size and provided with a lead keel mounted close to the float body to allow the antenna to maintain approximately 45° inclination to a flat surface. If the float were to be detached from a turtle and drift to a beach, it would be desirable to receive a directional signal from the float.

The following specifications apply to the 1970 float design shown in figure 1:

Length:	approximately 1 m
Diameter of body:	15 cm
Antenna length:	2.9 m
Weight in air:	9.3 kg
Balance:	The keel provides twice the righting movement of the antenna
Excess buoyance:	10 kg
Drag:	Approximately 1 kilogram at 1 meter/second
Attachment:	Iron wire is fastened to the caudal scute of the turtle's carapace. A braided polypropylene line, 21 meters in length, is attached between the wire fastening and the float.
Power supply:	Rechargeable nickel-cadmium batteries to provide approximately 30 days of operation.
Transmission:	10-second cw pulse every 10 minutes followed by a 15-second pause, then three series of pulses of 13 ms to code *X* and *Y* magnetometer sensing and velocity.

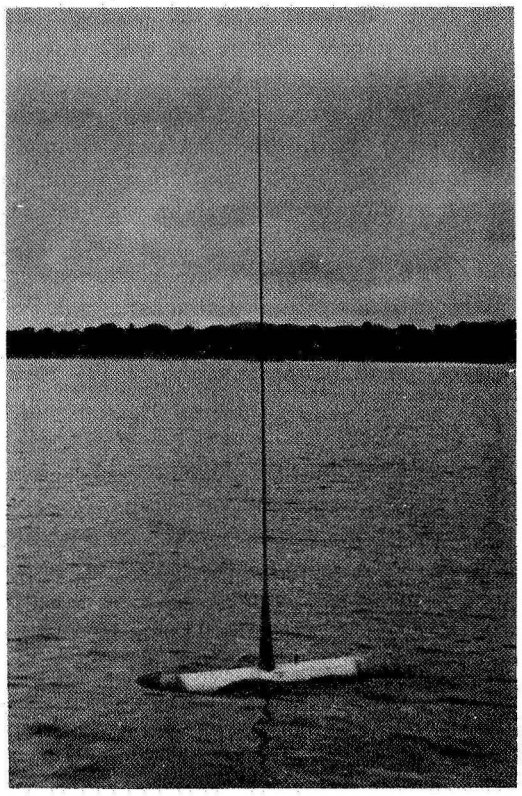

FIGURE 1. Transmitting float attached to a green sea turtle (not shown) to study path behavior during migration (summer 1970). The float transmits swimming speed and magnetic heading every 10 minutes.

A pilot experiment indicated satisfactory performance, with the exception that low speeds were not sensed. A venturi was placed over the paddlewheel velocity sensor to increase low-speed sensitivity. The minimum speed detectable with this feature was 0.27 meter/second.

EXPERIMENTAL RESULTS

Experiments 2 through 10 which are described below were conducted with the aid of a 16-meter motor vessel, the *Moderno*. Tur-

tles were displaced from the nesting beach various distances offshore and tracked by telemetry. The objectives were

(1) to investigate the "normal" behavior of a female turtle displaced away from the coast (nesting beach) and to establish the characteristics of its goal-directed homing ability;

(2) to investigate turtle path behavior under various weather conditions;

(3) to determine if, and under what conditions, small magnets might modify turtle path behavior.

The experiments which follow are numbered in chronological sequence. They refer to illustrations in the Appendix.

Experiment 1: Experiment 1 involved the release of an instrumented turtle from the nesting beach approximately 1 mile south of the entrance of the Tortuguero River into the Caribbean Sea (fig. 1). Investigators observed the behavior of the turtle and the float throughout the course of this experiment from a dugout boat (cayuca), approximately 10 m long and equipped with an outboard motor. The turtle swam outward from the beach at a comparatively rapid rate for approximately 30 min and then became quite inactive. The speed indicator on the radio float was not sensitive at these low speeds, and estimates of the actual swimming distance covering 10-min intervals were made by visual observation of the distance necessary to bring the cayuca back into the vicinity of the turtle. These distances are admittedly inaccurate. When they were significant, the time the boat was operated at a given motor speed was noted, and also a note with regard to whether the turtle was swimming, drifting or moving slowly was made in the record. If the turtle were moving significantly, the magnetic bearing data from the transmitter would correlate well with the actual heading of the turtle, but, during those periods when the turtle was inactive, the float at the end of a slack line very often took a heading somewhat different from that of the turtle. In addition to these interpretations of the turtle swimming behavior, the current along the beach was running at approximately 2 knots (4 km/hr). Periodic bearings were taken to various prominent terrain features such as Turtle Bogue Hill and the mountains approximately 28 km south of that hill.

The most significant observation was the fact that the turtle seemed to be inactive during the period when the sun was almost directly overhead. The experiment took place on September 4, 1970, at a time when the noon Sun position was 7° north of the equator. The latitude of Tortuguero is 10° 30′ north. Hence, for the period around noontime, it was not possible for the experimenter to orient with regard to the sun because of its near vertical position overhead. While sun compass orientation has not been demonstrated in *Chelonia mydas*, it must be strongly considered because of the importance of sun compass orientation to fish (ref. 4), birds (ref. 5), and possibly other migrating animals. The actual geographic movement with current covered some 24 km. The reconstruction of turtle path behavior is shown as though the turtle were swimming in still water.

Experiment 2: In this experiment we moved a turtle approximately 40 km offshore, beyond the edge of the continental shelf. By coincidence this turtle was the same one used earlier (tag number 6852) in September in experiment 1. She had been observed to nest successfully on two subsequent occasions and was captured after depositing eggs the second time. Nest locations were not dispersed more than 930 meters, so that one may conclude that the turtle was capable of remaining in the vicinity of the nesting beach in spite of the persistent current to the south-

east. The turtle was released at 1825 hr on the evening of October 2, just prior to a rain squall that obscured the sky. The turtle maintained an initial heading directly towards the nesting beach (west) although the beach itself was not visible and the sky was dark in that direction. The horizon to the east was clear. This turtle was remarkably consistent from the moment she was released until the float was lost from sight in the darkness in its direct heading toward Turtle Bogue Hill. Signals were obtained throughout the night and for the next 45 hrs. At approximately 2145 hr the rain squall broke and the stars became visible; within 20 min we noted a significant change in the direction from the telemetered path behavior data. During the morning of October 3, a second instrumented turtle (experiment 3) was released in the hope that the two turtles might take parallel paths in the same general direction. We soon found, however, that the turtles chose almost directly opposite headings and while we recovered signals from both transmitters during the day, we attempted to recapture the turtle heading out to sea. This attempt was unsuccessful, and we turned in pursuit of the turtle maintaining the westward heading. During the night of October 3, we heard a variation in the cw signal similar to those effected by handling the antenna, and soon thereafter the signal disappeared. The float was recovered several weeks later. The turtle had fouled the line in a drifting tree and submerged the antenna. The iron wire had eventually fatigued and released the turtle.

Experiment 3: This experiment shows the track of a turtle heading almost directly out to sea in a rather consistent manner. These turtles were released at the end of their nesting season, and it is quite possible that this turtle was returning to its feeding grounds somewhere in the Caribbean. As mentioned earlier, the float was not recovered.

Experiments 4 and 5: Experiments 4 and 5 were performed on the same turtle and are considered together because the experimental variable represented the presence of either a magnetic bar or a brass bar attached to the plastron of the turtle. Figure 2 is a sketch of the magnet assembly. The unit was made from Plexiglas and arranged to hold a bar magnet at its center of gravity so that it could pivot or rotate in a single plane parallel to the underside of the turtle. The concept of the device was to use the spinning magnet to test whether a changing magnetic field would be more disruptive to a turtle than a steady magnetic field. However, in experiments 4 and 5 this unit was placed on the plastron in such a manner that the magnet, while being free to move, did not actually

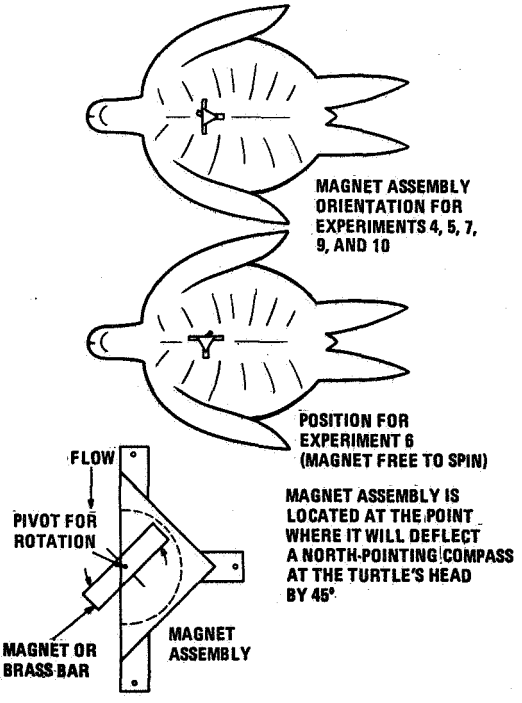

FIGURE 2. Details of attachment of magnets to the plastron of turtles.

rotate due to the flow of water past the attachment. The sketch shows this configuration for these experiments.

Experiment 5 was undertaken under similar conditions as experiment 4 with the exception that a brass bar of approximately equal size and weight replaced the magnetic bar. On both days the sun was visible and the weather was generally clear. Experiment 5 shows what we consider to be the normal heading toward the beach of a turtle displaced off the continental shelf. Experiment 4 appears to be a rather confused behavior pattern in comparison to the path reconstruction in experiment 5.

Experiment 6: This experiment was actually conducted in two parts and was intended to investigate the effect of a magnet on turtle path behavior during the hours of darkness. In this case the spinning magnet was placed in such a manner that the current passing by the underside of the plastron caused the magnet to spin rapidly. The turtle was released at 1450 hr some 37 km east of the beach beyond the continental shelf. The turtle was initially instrumented with the brass bar in place of the spinning magnet. Its path is shown for the period from 1450 hr to 1740 hr in a generally westerly direction after an initial escape circle to the east. After dark the turtle was recaptured and the magnetic bar was put in place of the brass bar on the turtle's plastron, still in such a way as to allow the current to spin it rapidly as the turtle swam. The float was also equipped at this time with a paddlewheel which produced a brief flash of light during each revolution. The turtle was released at 1745 hr and the flashing light was followed visually for a brief period of time. Suddenly, however, in the darkness the light ceased to flash at the same time the *Moderno* crossed a current boundary, noted by a heavy collection of sargassum plant and debris. We have assumed that the turtle also crossed this boundary and that the paddlewheel was fouled in the floating debris. The radio transmitter continued to report heading and velocity throughout the night. The track for the initial 2 hours showed a predominantly southerly heading. Then the track turned generally westward and eventually somewhat northwest during the next 2 days.

Early in the morning of the third day the turtle float was relocated by radio direction finding techniques and the turtle recovered near Limon, some 110 km southwest of the release point. The turtle experienced a strong southeast current during this time. At the time the turtle was recovered, the flasher was working in good order and the float was also performing as designed. The float had been out of visual contact since its release until actual recovery approximately 57 hr later. The turtle was found in a reef area whith is known by turtle hunters as a place where turtles are likely to be found. We have tentatively concluded that while the spinning magnet may have been responsible for disrupting the initial orientation of the turtle, it soon crossed over the well defined edge of the continental shelf and either disregarded the spinning magnet influence in favor of other guidance cues, or, if in fact it was sensitive to the earth's magnetic field, then the earth's magnetic field may have been distinguishable in spite of the rapidly changing field of the spinning magnet.

Experiment 7: This experiment was conducted within 2.8 km of the coast northeast of the port of Limon. In this case, the magnet was attached to the plastron in a fixed position; that is, it was not allowed to pivot but was tied rigidly in place so that the north magnetic pole was initially on the left side of the turtle. After 2 hr of data in which the turtle maintained a rather well defined steady bearing to the northwest against the current,

the turtle was recaptured and the magnet pole shifted so that the north pole was on the right side of the turtle. The turtle was released at 1125 hr in the morning and within an hour thereafter found a submerged reef. We therefore feel that this experiment was not valid in terms of the magnet as an experimental variable. It further supports our conviction that when water depths are low, that is, when the turtle has the bottom available, it uses reference to the available cues in preference to magnetic guidance.

Experiment 8: Experiment 8 was conducted on October 17. Its objective was to investigate the effect of the hauling in of a turtle on its path under the conditions where no other experimental variables are presented. The turtle was released at 1327 hr and maintained a general heading slightly north of west. At 1527 hr the turtle was recovered and again released. The path clearly demonstrates the initial escape behavior and the ability of the turtle to recover its desired heading within some 30 min after release.

Experiment 9: This experiment took place on October 18. Its objective was to test the effect of the continental shelf on a turtle equipped with a magnet in a fixed position on the plastron. The starting position for this experiment was 18.5 km off the coast where the depth was approximately 24 meters. The turtle was equipped initially with the magnetic bar and released at 0918 hr. The turtle maintained a heading to the northwest and was recovered at 1128 hr. The magnetic bar was then replaced with a brass bar and the turtle released at 1138 hr. After the initial 20 min, the path became almost parallel to the previous path. We therefore conclude from this experiment that the magnet did not have an effect on orientation at this distance from shore.

Experiment 10: Experiment 10 involved the same turtle as experiment 9, which had not demonstrated modification of path behavior by a fixed magnet on its plastron. We moved this turtle approximately 40 km from the coast. The turtle was released at 1549 hr and the reproduction of the path indicates a shift in general direction of 90° between the average direction of a path in experiment 9. This result reinforces our conviction that if sensing of the Earth's magnetic field is important to turtle orientation, then it is of primary value in water depth in excess of 180 meters.

DISCUSSION

The experiments reported above need to be replicated many more times before we can be sure that the experimental variables are those we believe them to be. From the work performed so far we can formulate the following conclusions:

(1) The green turtle can be counted on to maintain a reasonably constant heading (goal directed homing) when released in the sea, which might be characteristic of that individual but at least can be expected to be consistent. This suggests that the green sea turtle, with adequate instrumentation to reconstruct path behavior, is an excellent subject for the investigation of marine animal navigation theory.

(2) In the vicinity of Tortuguero there exists the possibility that turtles locate the region of their nesting beaches by olfactory cues. The experiments described above tend to weaken this hypothesis since in all of the cases where the turtles were displaced 37 km to sea they were introduced into water whose deep blue coloring identified it clearly as part of the Gulf Stream (the Mosquito gulf current) in contrast to the pale green water found over the continental shelf in this region. The boundary line between these currents was defined visually by lines of sargas-

sum rafts which included floating logs and other debris. There seems to be little opportunity for the laws of diffusion to apply across such a well defined shear line with water on both sides of the shear line moving at quite different rates of flow. In our experiments we observed turtles crossing this shear line without any change in heading or speed. We therefore feel that the chemical content of the water itself is of little importance in orientation under these conditions.

(3) The effect of the placement of a magnet on a turtle produced a dramatic change in the path behavior of turtles released beyond the continental shelf. We are reluctant to state, however, that the experiments are statistically significant as independent events since we have only two observations. We are also reluctant to consider the 10-min intervals as independent observations. However, taking the paths as a whole there is a very strong conviction that in experiment 4, with the magnet free to pivot, the turtle's path can be classified as not oriented. The path in experiment 10 seems to produce an error of 90° that would be predicted from the placement of a magnet in a fixed position on the plastron. These observations are consistent with the hypothesis that turtles sense the Earth's magnetic field as a primary orienation cue in deep water.

Circuits used in the telemetry of turtle path behavior are shown in the Appendix.

POLAR BEAR INSTRUMENTATION

In the spring of 1970, the initial attempt was made to track polar bear on the polar ice cap north of Barrow, Alaska. Jack W. Lentfer had developed techniques of immobilizing bears using a helicopter (ref. 6) and had marked approximately 200 wild bears in previous seasons. Opportunity to work with these animals is restricted to spring months after the dark of the polar winter begins to disappear and before the sea ice recedes from the northern coastline of the Arctic region. Easy access to the ice cap is primarily limited to the range of light aircraft, and the instrumentation selected was based on the need to track radio tagged bears from the air. A VHF frequency, 148.5 MHZ, provided a short enough wavelength to allow the use of directional antennas mounted on a wing strut, and an electrically short collar antenna provided an omnidirectional signal for line-of-sight ranges greater than 185 km.

Figure 3 shows a radio tracking collar for polar bear prior to final sealing and waterproofing. The lower portion contains silver-cadmium rechargeable batteries for low tem-

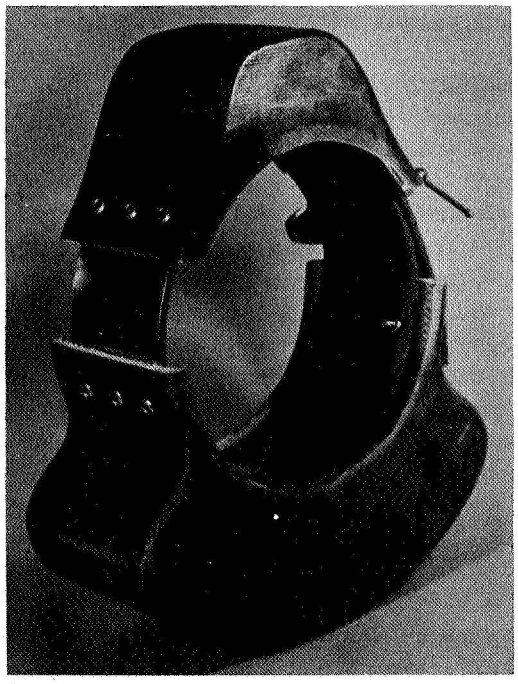

FIGURE 3. Polar bear radio collar during construction. Collar is made from machine belting, and electronic equipment is covered with fiberglass and embedded in foam.

perature operation to —60° F, and a small transmitter. The upper portion contains a low profile antenna. This antenna is approximately 2.5 cm in height and is embedded in low-loss dielectric foam to eliminate the possible loading effect of ice or sea water. The weight of the collar is approximately 2.3 kg.

Six transmitters were constructed and fastened to polar bears during the spring of 1970. One transmitter was removed when a bear was killed by hunters and was reused on a seventh bear. The longest track was approximately 150 km in a period of 23 days. Contact was made in this case on three occasions after release. Flying time was severely limited by weather conditions.

The greatest range for radio detection under field conditions was approximately 56 km. This is in contrast with tested ranges of 213 km with the transmitting collar placed on the ice and the receiver in an aircraft at 2440 meters above the ice. The lack of agreement may be due in part to the presence of ice pressure ridges, bear movements or body positions, and possible ducting effects due to the strong temperature inversion over the polar ice. In addition, subsequent testing indicated antenna detuning due to the high conductivity of polar bear fur after immersion in sea water.

The receiver system for use in the aircraft is shown in figure 4. The receiver is a narrowband (4 kHz) high-gain circuit optimized to receive and detect transmitter pulses of about 13 milliseconds in length. All transmitters operate on a single frequency and individual units are identified by their pulse period. The interval timer was used to help rapidly identify the pulse rate. Two receiving antennas were used: a commercial three-phase element yagi[3] for long-range unidirectional detection (fig. 5), and a dual half-wave antenna for detection of a null bearing by interferometry (fig. 6). Figure 7 shows a radio collar being fitted to the neck of a large female polar bear. The circuit for the transmitter is shown in figure 8.

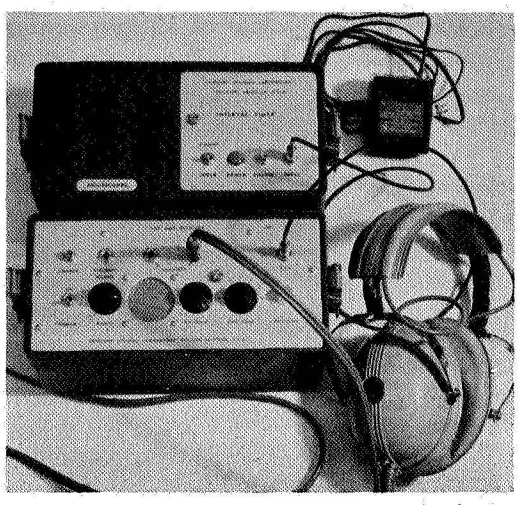

FIGURE 4. Tracking receiver for use in light aircraft. Interval timer allows for rapid identification of the pulse rate of an individual transmitter. All transmitters operate on same frequency since bears are dispersed.

FIGURE 5. Directional high-gain antenna for long-range detection of VHF signals.

It is too early in this program to interpret the significance of the tracking data obtained so far with polar bears in the vicinity of Point

[3] HyGain Model 23.

Barrow. The movement of all instrumented bears to the northeast during the spring seems to be part of an annual pattern, however, observed by hunters and Eskimos in previous years. One of the bears captured for instrumentation had been tagged 2 years earlier very close to the same location. Longer periods of observation at greater distances from Point Barrow will be required to establish a significant portion of the annual polar bear migration routes, if they exist.

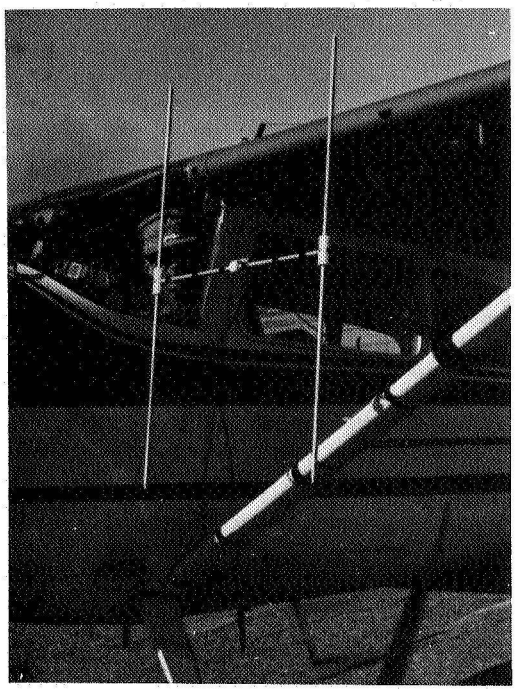

FIGURE 6. Interferometer antenna for detection of null bearings for accurate location of radio-tagged polar bears.

FIGURE 7. Radio collar being fitted to the neck of a large female polar bear.

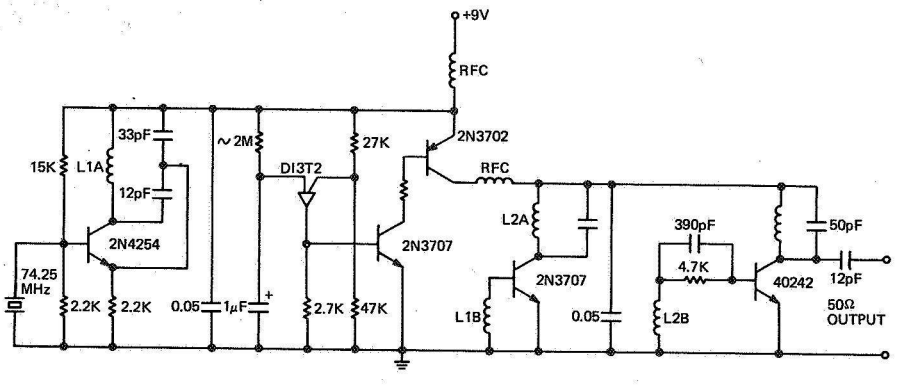

FIGURE 8. Circuit diagram for VHF (148.5 MHz) polar bear transmitter.

APPENDIX

TRACKING DATA AND CIRCUIT DIAGRAMS FOR TURTLE PATH TELEMETRY

Figures 9 through 18 show turtle tracking data by experiments referred to in the text. Figures 19 through 25 describe instrumentation used in these experiments.

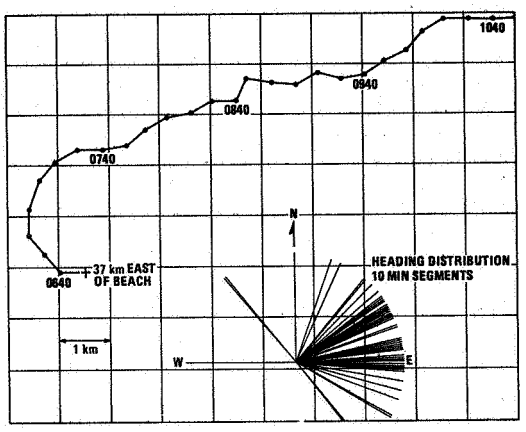

FIGURE 11. Experiment 3, October 3, 1970.

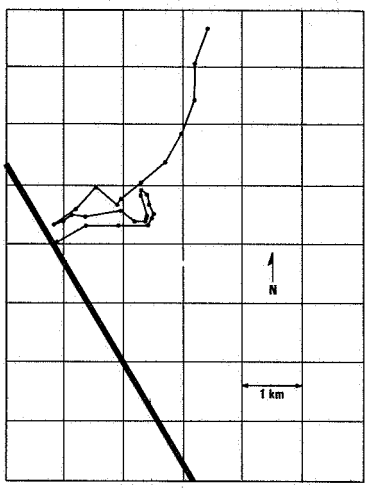

FIGURE 9. Experiment 1, September 4, 1970, without current.

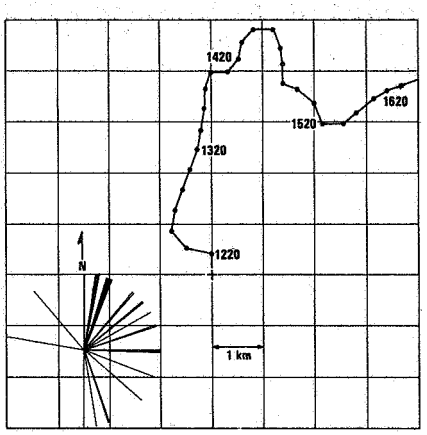

FIGURE 12. Experiment 4, October 9, 1970, fixed magnet.

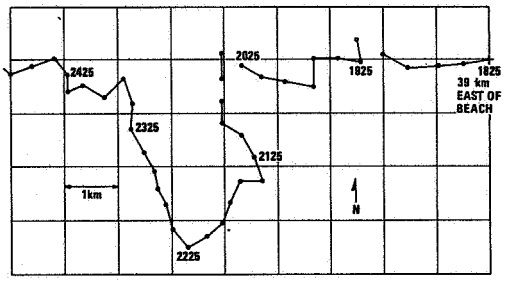

FIGURE 10. Experiment 2, October 2, 1970, sky obscure until 2145 hours.

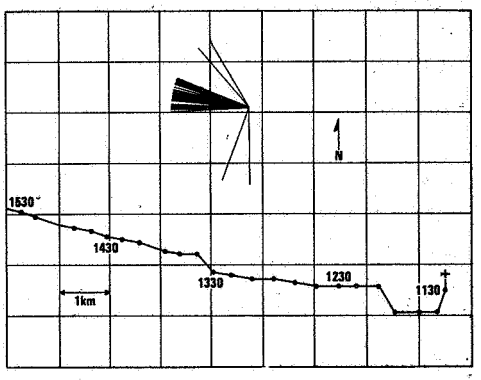

FIGURE 13. Experiment 5, October 10, 1970, brass bar.

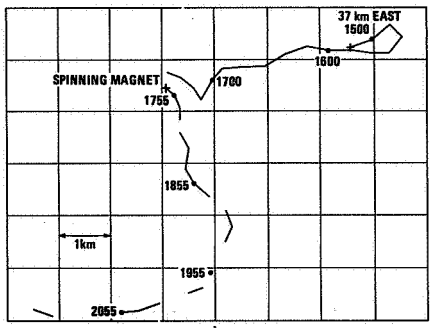

FIGURE 14. Experiment 6, October 12, 1970.

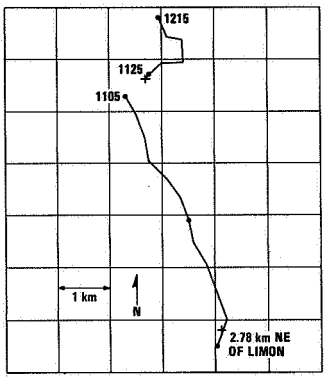

FIGURE 15. Experiment 7, October 15, 1970, fixed magnet.

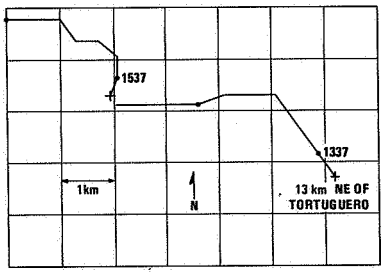

FIGURE 16. Experiment 8, October 17, 1970.

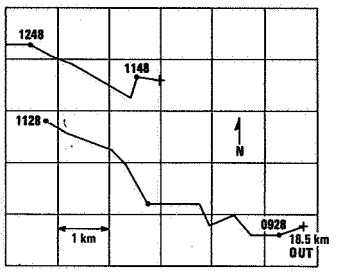

FIGURE 17. Experiment 9, October 18, 1970, fixed magnet.

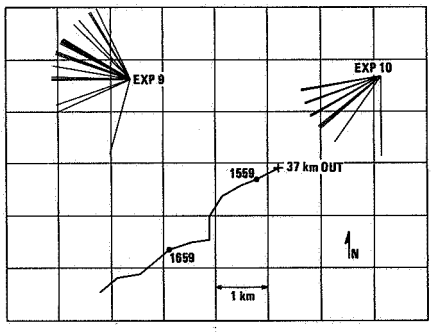

FIGURE 18. Experiment 10, October 18, 1970, fixed magnet

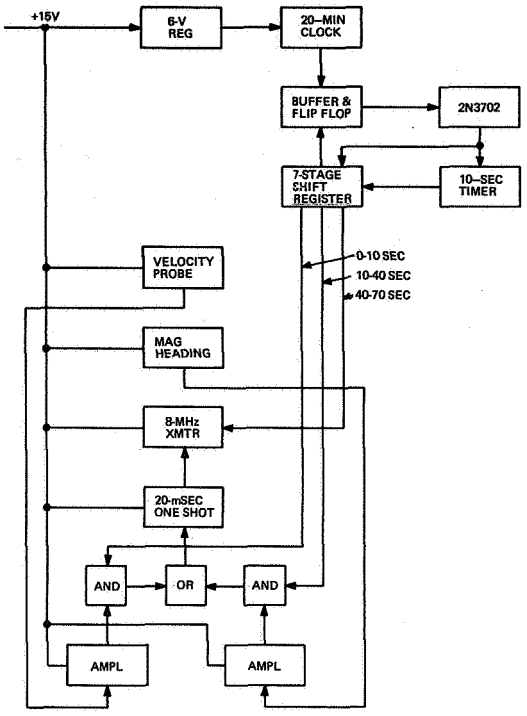

FIGURE 19. Block diagram of turtle float clock.

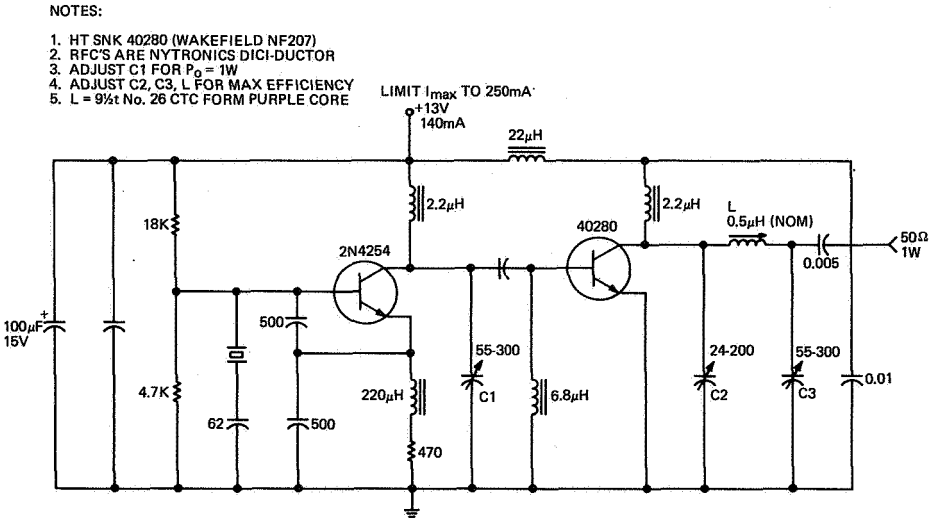

FIGURE 20. Circuit diagram of 8-MHz transmitter.

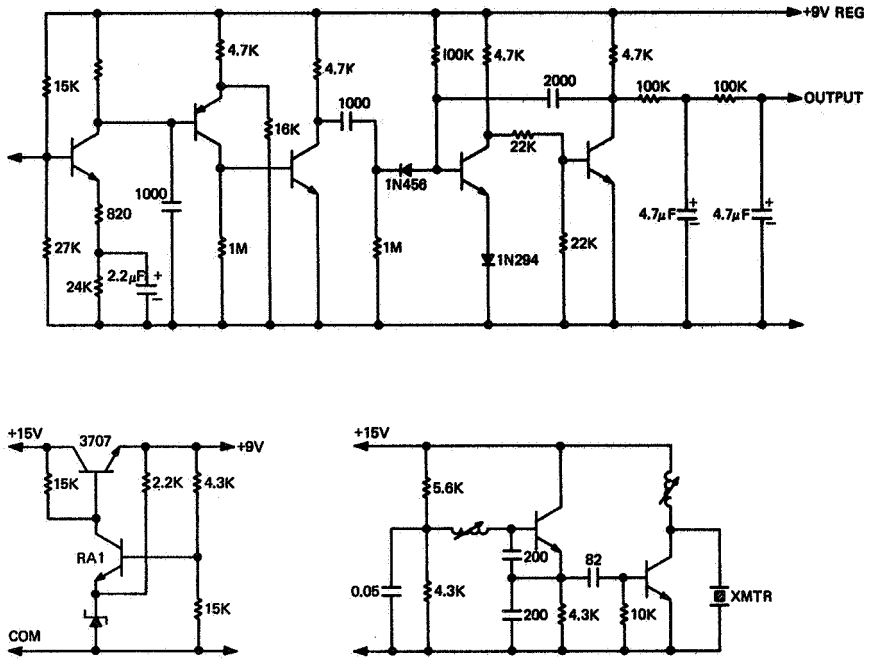

FIGURE 21. Circuit diagrams of Doppler velocity decoder, regulator, and transmitter.

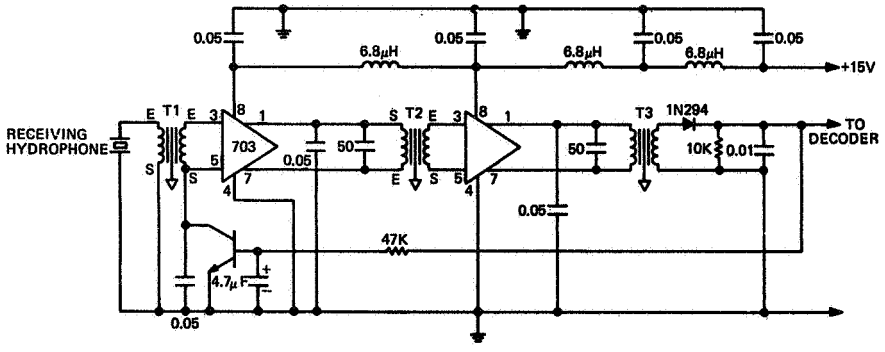

FIGURE 22. Circuit diagram of Doppler velocity-meter receiver.

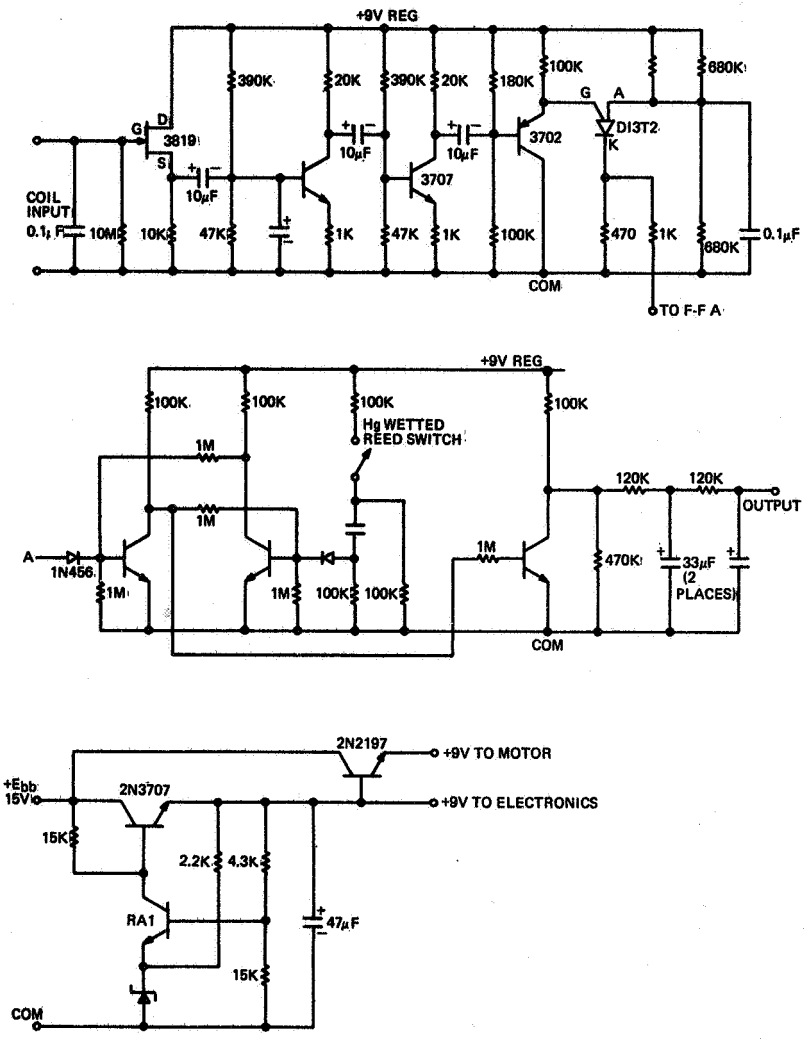

FIGURE 23. Circuit diagram of magnetometer compass.

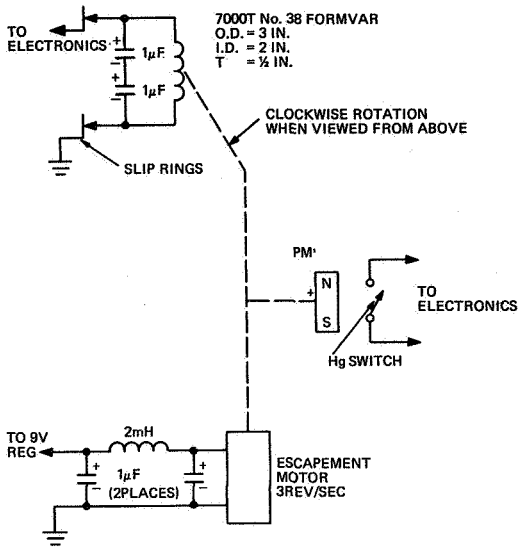

FIGURE 24. Schematic diagram of magnetometer compass.

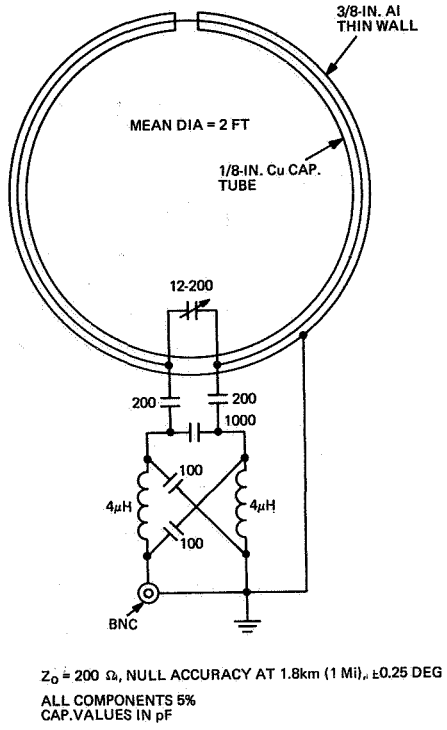

FIGURE 25. Schematic diagram of 8-MHz DF loop.

DISCUSSION

QUESTION: Would you please give more details concerning the release and heading of the turtles?

BALDWIN: Dr. Carr has described his hypothesis with regard to turtle navigation from the coast of South America to Ascension Island. Basically he has assumed that the westward drift of current past the island would carry a chemical cue discernible by turtles swimming against the westward drift to help them localize their goal—that is, Ascension Island. Dr. Carr, therefore, proposed displacing a turtle to the north of the island to avoid any guidance cues related to olfaction. Our telemetry system indicated that the turtle chose a heading directed toward Ascension immediately upon being launched from the ship, 187 km northwest of the island. However, we received data from the float for only 2 hours, and while this heading or azimuth data was consistently toward Ascension, we do not at this time feel that it is sufficiently convincing to rule out the olfactory orientation hypothesis for Ascension Island.

MACKAY: Do you think it would make any difference if the float were attached to a swivel above the center of mass of the turtle? Then, if there were a current, the torque would not keep twisting the turtle away from his chosen direction and into the current, as when the line is attached toward the end of the shell. It would seem that sort of a "crabbing" operation would be required to move in a preferred direction if the attachment was wrong.

BALDWIN: We have measured the drag of the transmitting float at approximately 910 grams of force at 0.9 meter per second velocity. This is certainly a minor drag for such a powerful swimmer as a mature green turtle. Furthermore, the attachment to the shell is made along a line running through the center of gravity of the turtle; there would, therefore, be no tendency for the float to modify the swimming direction of the turtle.

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Long-Distance Tracking of Birds

WILLIAM W. COCHRAN
Illinois Natural History Survey

GRIFFIN (ref. 1) phrased a need,

> It would obviously be helpful to know more about actual routes flown by individual migrating birds. If we had a number of accurate maps showing just where particular birds had flown on long migrations, we might be able to identify important factors influencing the timing and orientation of these flights.

and commented on a means,

> Glamorous press releases depict the tracing of barn swallows by radio receivers from North to South America, but in fact the limitations of this method are still severe. For the next few years radio telemetry of migrations seems likely to be limited to birds of the size of pigeons or larger.

Months later Graber (ref. 2) and Cochran, *et al.* (ref. 3) began following hylocichlid thrushes, a bird one tenth the size of a pigeon, on flights as long as 650 km (400 mi). Since that time some 11 000 km (7000 mi) of bird tracks have been recorded; some of these are shown in figure 1. However, for a migrant traveling several thousand or more km, a track of several hundred kilometers reveals little of a bird's orientation or navigation performance in terms of its goal and origin and less yet of its response or lack of response to the variety of stimuli that may come into play over such a long journey. Long-distance tracking is here considered as the following of an individual bird over a substantial portion, or ideally over all, of its migratory journey. This includes numerous flights interspersed with stop-overs along the way and involves weeks or even months of surveillance. This tracking has not yet been done, but the experience that has been gained and evolution of equipment and technique that has transpired since 1965 have made the following of birds for thousands of km a matter of desire and funding rather than a question of possibility. Some of the ingredients of long-distance tracking are discussed below. The purpose of this paper is to describe the radio-tracking technique and not to disucss the meaning of the conglomeration of bird tracks illustrated. The latter must include other data not shown and will be the subject of other papers.

BIAS

Perhaps the greatest single problem to be encountered in carrying out long-distance tracking is the problem of bias to the subject bird. It seems axiomatic that the use of telemetric devices on birds will affect their performance. This will be true whether attachment is by harness, implant, or adhesive, and

no matter how small or light-weight the device is, or how comfortable it appears. Griffin (ref. 4) stated that

> Long-distance navigation shows some signs of being a pattern of behavior that is sensitive to even minor disturbing influences, and if it is to be studied effectively by telemetry, one must be sure that the radio tag is not distorting grossly the behavior pattern under study.

Further,

> The usefulness of radio telemetry will be much enhanced: that is, we will obtain more and better data from its use, the smaller the transmitter package (including batteries and antenna) relative to the marked animal. Ideally it should be not more disturbing than a bird band. It should be possible to attach the unit, release the bird within a few minutes, and have its behavior return to normal within a few hours.

What more can be said?

For a given species and study objective, a bias may be acceptable if it were known. Unfortunately quantitative evaluation of bias is difficult. Because telemetry affords numerous opportunities for visual observation of the subject, a qualitative estimate of behavioral bias can be obtained by comparing these observations with less frequent but similar observations of non-tagged birds of the same species. Or one may note obvious abnormalities such as inability to fly, or concentrated and sustained attention to removal of the transmitter. Also, progress or lack of progress in migration as compared with the species as a whole can function as an indicator; imagine having the only live Swainson's thrush in all of North America under observation in January!

There are numerous ways in which a transmitter may affect a subject bird. Weight of the transmitter and degradation of a bird's streamlining increase the energy required for flight. Shifts in a bird's center of gravity may cause even greater increases in energy requirements through alteration of the trim required for horizontal flight. Perhaps some species or individuals are of such a temperment that the mere presence of a foreign

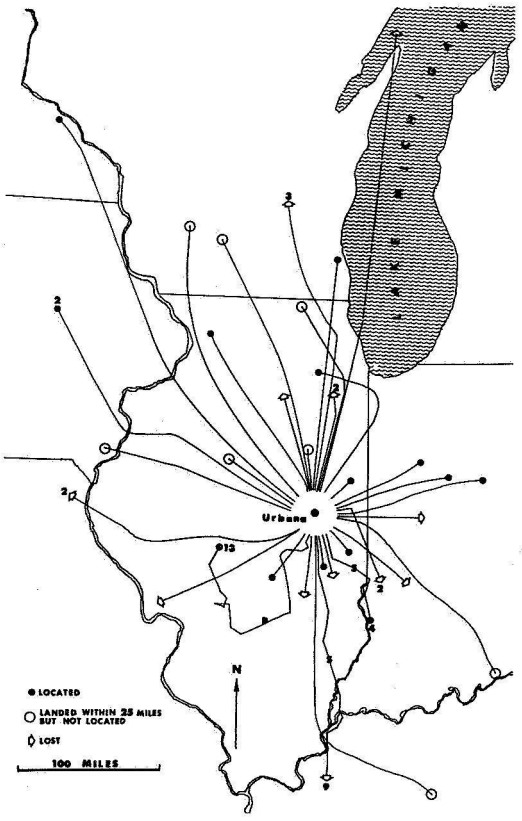


FIGURE 1. Summary of approximate flight tracks as determined by telemetry for the flights from Urbana, Illinois. All tracks within arc from east through south to southwest are fall flights; all others are spring flights. All flights are of hylocichlid thrushes except the two marked *S* (sharp-shinned hawk), and the one marked *P* (homing pigeon). Random nature of pigeon flight contrasts with migratory flights and suggests that many of the methods described in the text would not be useful for tracking this type of flight. Numbers at end of tracks are number of separate flights making up the track; no number indicates one flight.

object on their body affects their behavior in ways not related to physical factors.

For long-distance migration studies, the cumulative effects of these or other forms of bias must be considered. For birds observed for a few days or for one flight, the bias, as long as it is not severe, may not measurably affect performance. However, for studies involving long distances and weeks or months of observation, it is possible that the effects of a small impediment to a bird may accumulate until the bird becomes physically incapable of performing normally. The data given in table 1 for swans, geese, thrushes, and hawks indicate considerable hope for their long-term study, while for others such as the sandpiper and cowbird, it appears that such studies are impossible with present techniques.

ATTACHMENT

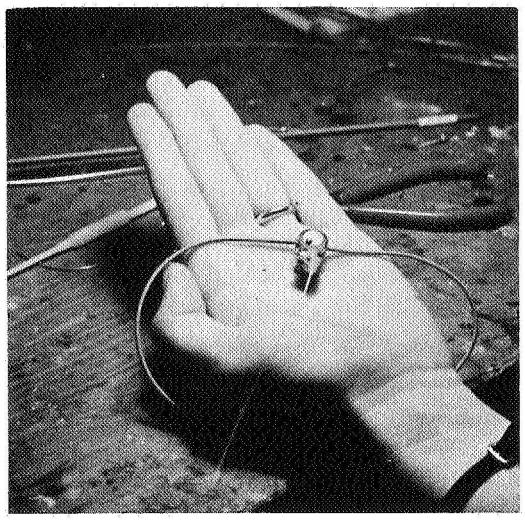
Numerous methods of transmitter attachment have been tried on a variety of species, and it appears that no one method is universally satisfactory. Adhesive only, single-wire harness only, and two-loop harness as well as thin-fabric and thin plastic sheets with wing holes were all tried on the hylocichlid thrushes. The adhesive did not last for more than a few days, and the single-wire harness fell off after 3 to 8 days. The double-loop harness and thin-sheet harnesses impeded flight. After several years of marginal results, a combination of adhesive (Eastman 910) and the single-wire harness was tried with immediate success. This attachment method usually outlasts the battery which has a 20- to 35-day life. One Swainson's thrush was observed for 2 weeks including two migratory flights lasting about 8 hours each; it was then recaptured and examined. It weighed 34 grams, 1 gram less than when initially captured, and showed no signs of abrasion or other ill effects. The adhesive and harness wire were still holding well.

The attachment is made as follows: Attached to the transmitter at its mid-point are two stranded, plastic-covered wires. The wire is very flexible. After having first affixed the transmitter with adhesive as described by Cochran et al. (ref. 3), the two wires are brought under and behind the wings and in front of the hips, worked into the feathers a little, and then tied with a square knot. Figure 2 shows some of the procedure.

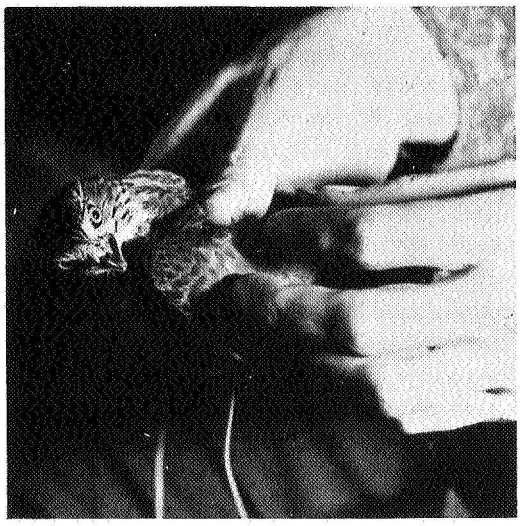
EQUIPMENT

Principle transmitter variables are weight, battery life, and radiated power. Permissible weight has been touched on above; since it can not be too light, it should be as light as possible. The battery life required will depend on how long one desires to maintain contact with the subject without having to recapture it for transmitter replacement. Since frequent recapture and handling would certainly be an additional bias, the battery should last as long as possible. Although I might settle for a week, I am quite happy with the 20 to 35 days the most recent transmitters have been giving. Radiated power between 0.1 and 0.5 mW in the VHF or UHF frequency range will provide an operating range of more than 24 km (15 mi) to birds in flight. Several transmitters are shown in figure 3.

After having established that the smallest and lightest available components are used in construction and that the circuit used achieves near state-of-the-art energy conversion, further improvements in any one of the variables can be achieved only at the expense of one or both of the others. In engineering language, "trade-offs" must be made. Unfortunately many of the commercial and homemade units are not optimized with respect to



A



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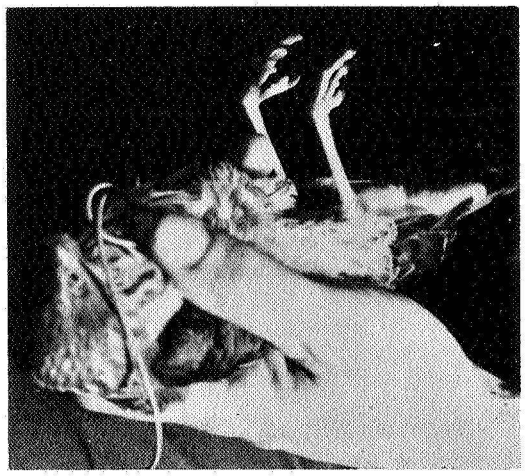

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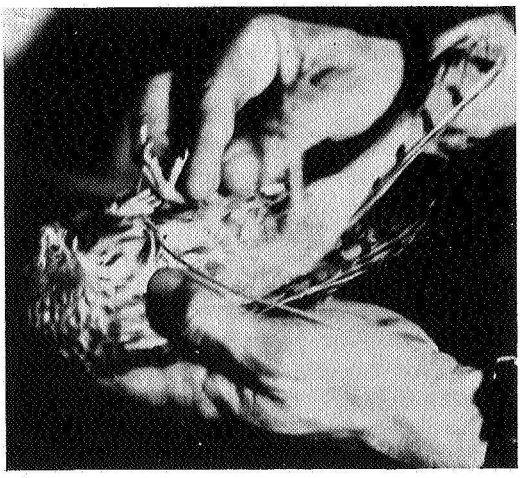

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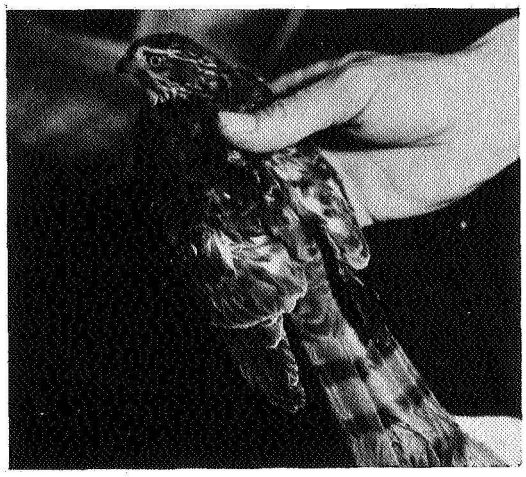

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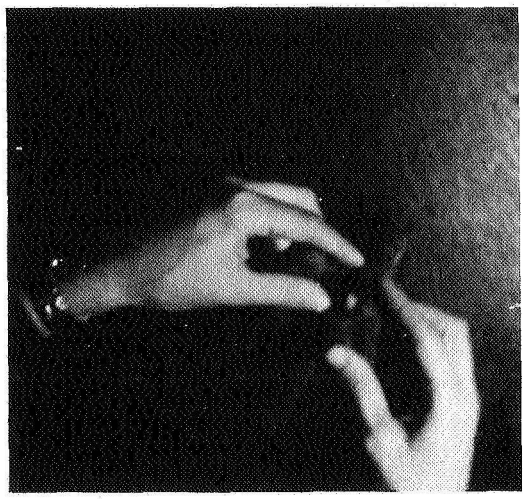


F

G

FIGURE 2. Installation on sharp-shinned hawk and hermit thrush: (A) transmitter—3.5g; (B) transmitter held to back while adhesive sets; harness wires have been run behind wings; (C) turned over, knot started; (D) knot almost completed; excess to be cut off; (E) ready to be released; (F) hermit thrush with 2.3g transmitter in place; and (G) ready for release.

TABLE 1.—*Summary of Various Bird Species Radio-Tagged by the Author*[a]

Species	Number observed	Approximate tag weight in % of body weight	Maximum flight distance observed	Maximum duration of observation in days for one individual	Estimate of annoyance	Types of attachment
Whistling swan (*Olor columbianus*)	25	1	1600	120	Occasional	*X*
Canada goose (*Branta canadensis*)	30	1	400	28	Occasional	*X*
Mallard (*Anus platyrhynchos*)	5	1.5	[b] 50	2	Occasional	L, *X*
Blue-winged teal (*Anus discors*)	2	3	[b] 25	5	Frequent	[c] W
Brown-headed cowbird (*Molothrus ater*)	1	8	[d] 2	3	Frequent	[e] WG
Gray-cheeked thrush (*Hylocichla minima*)	23	8	400	12	Seldom	[c] F, [f] G, [e] X, W, *WG*
Swainson's thrush (*Hylocichla ustulata*)	30	8	375	14	Seldom	[e] F, [f] G, [e] X, W, *WG*
Veery (*Hylocichla fuscescens*)	9	8	460	13	Seldom	[e] F, [f] G, [e] X, W, *WG*
Hermit thrush (*Hylocichla guttata*)	19	8	250	20	Seldom	[e] F, [f] G, [e] X, W, *WG*
Robin (*Turdas migratorius*)	5	4	[d] 5	5	Occasional	[e] F, G
Sharp-shinned hawk (*Accipiter striatus*)	3	3	250	15	Seldom	*WG*
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	1	4	(g)	5	Seldom	*WG*
Yellow-shafted flicker (*Colaptes auratus*)	4	3	[d] 10	5	Frequent	[e] W, [f] G, [e] WG
Pectoral sandpiper (*Erolia melanotos*)	2	5	(h)	(h)	.....	[h] WG
Homing pigeon (*Columbia livia*)	10	1.5	[b] 200	9	Occasional	L, *W*

[a] The next-to-last column gives a qualitative estimate of the frequency with which individuals pecked or pulled at the transmitter or harness. The estimate is based primarily on visual observation. The last column is type of harness tried; *those in italics* seemed satisfactory.

[b] Displaced birds; flights not migratory
[c] Birds could not fly well
[d] Local movements
[e] Transmitters known to have been removed by sustained efforts of the bird
[f] Transmitters usually fell off
[g] Departed on migratory flight but was not followed
[h] Could not fly with transmitters; transmitters removed
X 2-wire harness
L taped to leg
F fabric or plastic wing harness
W single wire harness
G Eastman 910 adhesive
WG wire plus adhesive

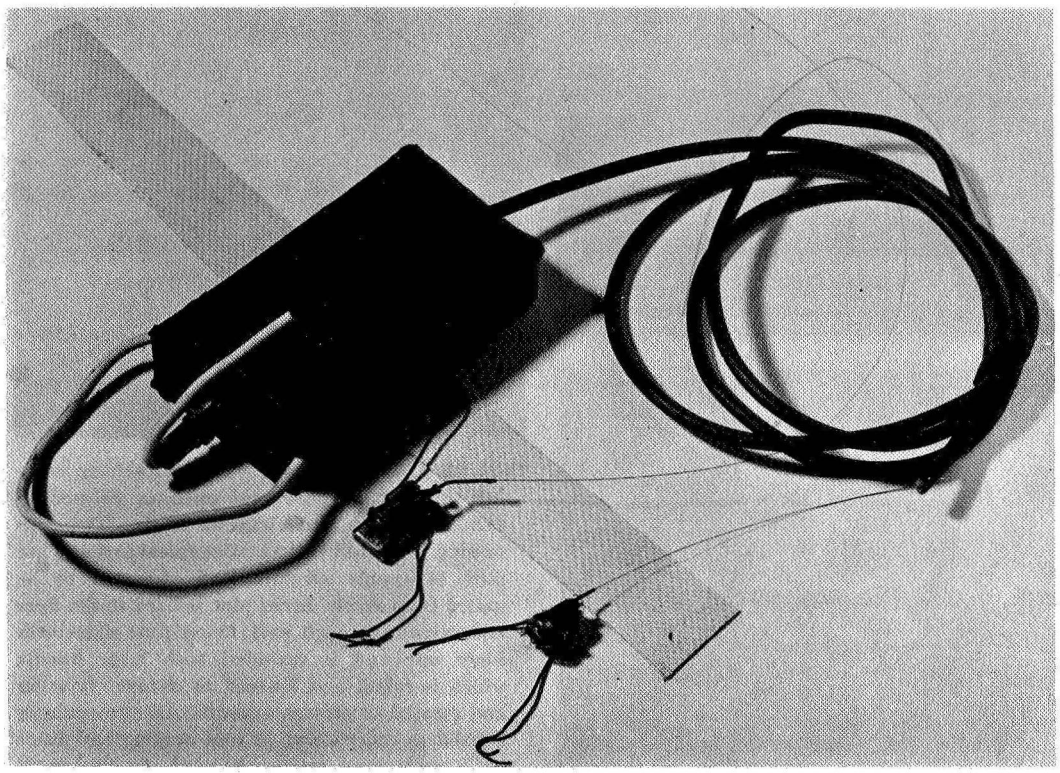
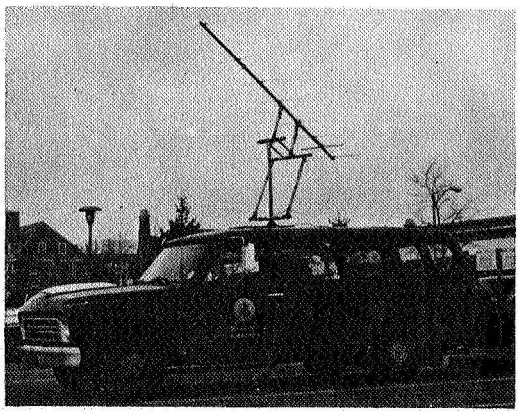


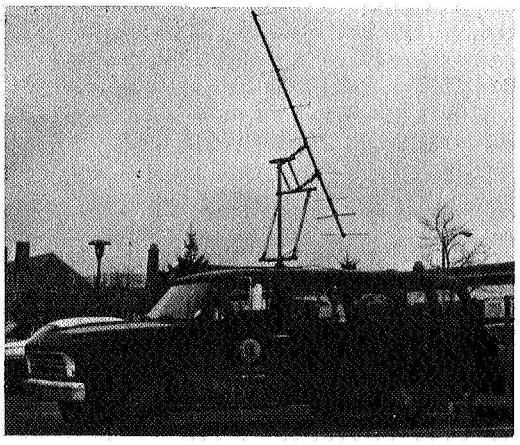
FIGURE 3. Three transmitters designed for birds. Left is 70g unit designed (but never used) for pigeons, which is similar to those described by Singer (ref. 5). Middle unit is of type used for most all work described in the text. Weight is between 2.2 and 2.4g; battery lasts for 25 to 35 days. An earlier version of this design is described by Cochran (ref. 6). To right is a 1.5g unit first used in 1970; except for weight it is similar to the 2.4g design. Both small transmitters were removed from thrushes after flights. Transmitters are shown 1/2 actual size.

either circuit or components and may miss the optimum by a factor of more than 10 if all three principle variables are considered simultaneously.

A receiver and receiving antenna are required. Sensitivity, frequency stability, reliability, portability, and a good ignition-noise silencer are probably the most important considerations in choosing a receiver. Six- or eight-element yagi type antennas are of convenient size for mounting atop a vehicle (fig. 4) and two- or three-element yagis are easily attached to the foot step or struts of small planes (fig. 5). Both provide sufficient gain and directivity to enable one to follow migrating birds. With a 16-element array mounted atop a 30.5-m tower, I have maintained signal contact with birds at distances up to 110 km (70 mi); but, of course, such installations are of little use because of their lack of portability.

Possession of suitable equipment is necessary but hardly sufficient to accomplish tracking of migrating birds over long distances. This is analagous to a fine sword not making a fine, or even tolerably poor, swordsman. It





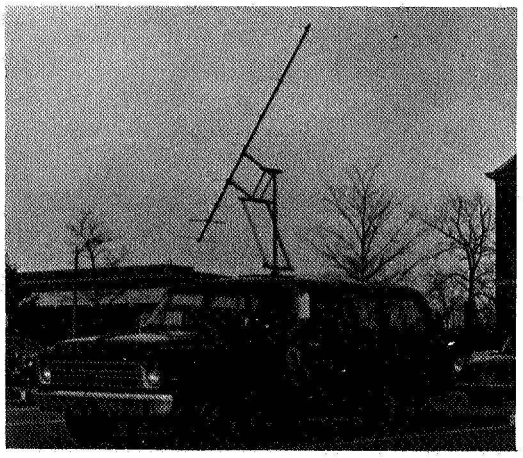


FIGURE 4. Several views of tracking vehicle showing the eight-element yagi antenna pointed at various azimuth and elevation angles. Two telescoping pipes and various mechanical linkages are used to enable azimuth and elevation to be varied from inside. Inner pipe is fixed to the floor and extends through roof. Outer pipe slides over inner one and is provided with large handle which is raised and lowered to change elevation and rotated to change azimuth. Azimuth pointer is fixed to inner sleeve of roof bearing and reads on a scale over operator's head. In horizontal position (elevation of 0°), clearance is 11 ft.

is surprising how few persons have the ability to rapidly read road maps, know their right from their left flawlessly, or relate right or left to map direction. One must also be able to scale distances and plot bearings on maps, to know how to add, subtract, multiply and divide, and to be able to read time from a clock. Lest one think I am trying to be funny, I might add that were it not too embarrassing to my colleagues and myself, I could take each of those functions mentioned above and describe how a bird was lost through human error in its performance. Repeatedly performing correctly for periods of up to 10 hr when one would normally be sleeping but instead is bouncing along a road or riding in a noisy airplane is not quite as easy as it might seem, and it is harder still unless one acquires the ability to perform almost without thinking. It is appropriate to mention here that birds can be followed by using a

TABLE 2.—*Typical Range (Miles) to 0.25- and 2.5-Milliwatt Transmitters on Birds as a Function of Altitude or Location of Both Bird and Observer*[a]

	Range (miles)			
	0.25-mw transmitter		2.5 mw-transmitter	
	Airplane at 3000 feet	Vehicle	Airplane at 3000 feet	Vehicle
On the ground in open, relatively flat terrain	4	0.5	.....	1
On the ground in heavy woods	2	0.25	.....	.....
On a large body of water	18	.....	35	6
A few feet off the ground in open, relatively flat terrain	6	1	.....	4
A few feet off the ground in heavy woods	4	0.75	.....	.....
In a high tree in open, relatively flat terrain	20	8	45	20
Near the top of the canopy in extensive woods	10	3	20	5
Flying, 100 foot altitude	25	10	45	15
Flying, above 3000 feet	45	30	100	50

[a] In rolling terrain values may vary +20 percent to −90 percent from those given, depending on whether the transmitter is on a hill or in a valley. In mountainous terrain visual line-of-sight closely predicts transmitter range which will therefore be highly variable.

system, not just equipment, and that the system includes human operators with proficiency in these skills and knowledge of the techniques which are described below.

OPERATING RANGE

The maximum operating range to radio-tagged birds can vary by a factor of at least 100. Some of the ranges and conditions for which I have test information are given in table 2. These ranges are typical for signals radiated within 45° of a right angle to the transmitting antenna. Weak and fluctuating signals are radiated along or near the axis of the antenna. Since the antenna trails behind a bird in flight, it is a distinct disadvantage to fall behind in tracking. Fortunately the solid angle of weak or no signal is not large, giving range reductions of a factor of 5 or 10 for only about 10°. In fact, the null area is so small that when driving across a bird's track, either in front of or behind the bird, at a distance of 8–16 km (5–10 mi), the signal will be weak or undetectable for only a minute or less. Furthermore, the true bearings

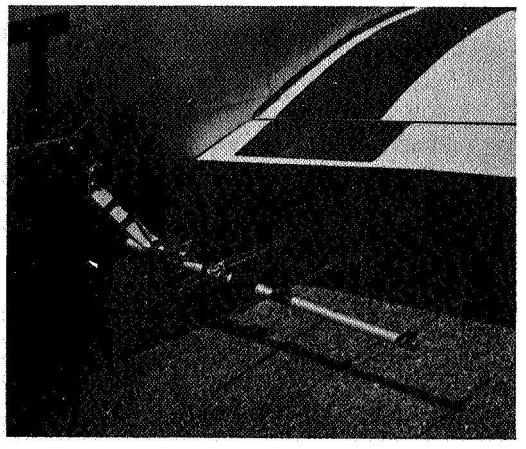


FIGURE 5. Two hose clamps hold three-element yagi to footstep of a Piper Arrow single-engine airplane. Coaxial lead is taped to footstep support and enters airplane through corner of luggage compartment door.

taken while crossing fore or aft of the bird will give its heading. Headings taken in this way have been typically within 10° of those calculated from bird track and concurrent winds-aloft information.

The reliable air-to-ground range of only 3 km (2 mi) to a transmitter in heavy woods dictates that a thorough search of a large area by airplane can be quite expensive.

ESTIMATING RANGE

The great influence of bird altitude and aspect on signal strength dictates that signal strength by itself is a very poor indicator of range. Still, with experience, it is possible to categorize range, with respect to the signal-to-noise ratio, as less than about 8 km (5 mi), 8 to 24 km (5 to 15 mi), or 24 to 48 or 64 km (15 to 30 or 40 mi). This may be supplemented by rate of change of bearing information. For example, if the vehicle speed is on the order of 0.8 km/minute (one half mile per minute) or more relative to bird speed and the vehicle is approximately paralleling the bird track, the bearing will change slowly if the bird is far, and rapidly if it is close.

TAKING A BEARING

Taking a bearing requires comparing the signal amplitude for various angular positions of the receiving antenna. With an eight-element yagi, signal amplitude begins to drop very sharply about 20° either side of the true direction so that achieving an accuracy of ±20° requires only one or two sweeps of the antenna. The limit is ±1 or 2° and this only from a stationary vehicle and after averaging the results of numerous sweeps of the antenna. Fluctuations caused by passing terrain limit accuracy obtained from a moving vehicle or to a low flying bird to ±4 or 5°. Since these are errors in bearings taken relative to the vehicle, the true bearing will include an additional error in measuring the vehicle's heading. When using accurate maps or when the vehicle can be aligned with the north star or a straight road, the added error need not be greater than 1 degree; but, when working with a magnetic compass or ordinary road maps in some areas, errors may be several degrees or even more if one is careless or in a hurry.

Bearings can be obtained from an airplane by observing the signal amplitude while circling. Because the directional pattern of a two- or three-element yagi is quite broad, and asymmetry of the airplane (for side searching antennas) causes distortion of this pattern, errors of 15 to 25° are typical.

ALTITUDE DETERMINATION

The ideal method for obtaining altitude information on birds carrying tracking transmitters is to telemeter the air pressure. If this were accomplished with a resistive transducer which modulated the transmitter pulse rate, then measurements of altitude could be made on a relatively continuous basis as long as the tracking vehicle was within signal range. The only equipment needed would be the second hand on a wristwatch. Unfortunately a barometric transducer has not been developed whose resistance changes at least 1 percent for every 2 percent change in absolute pressure and whose weight is a fraction of a gram. However, such devices may be quite feasible if the weight limitation were increased as appropriate for larger birds.

As has been discussed above, a crude estimate of range can be made on the basis of signal strength, if one assumes that the bird is high or low. Inversely, if the range is approximately known, then a crude estimate of altitude can be made. This was done regularly

during the spring of 1966 but later, when the method described below was used as an independent check, I found that the accuracy was much worse than anticipated but still sufficient to categorize altitude as high, low, or landed. Of course, no sharp dividing line exists between the qualitative terms high and low. In practice the concept is valid if one accepts low as 30 m (100 ft) and high as 300 m (1000 ft) with the altitude range between as a transition zone. To restate: If the signal is weak and fluctuating at 16 km (10 mi) range the bird is low, and if strong and steady at this range the bird is high.

By providing means for orienting the receiving antenna in elevation angle from 0° (horizontal) to 90° (vertical), altitude may be obtained geometrically. There are numerous combinations of measurements of elevation angle, bearing, distance, and time which will yield altitude. If simultaneous observations are made from two places, the method is exact (although the measurements will not be). If all observations are made from a single tracking vehicle, there will always be at least one inherent assumption. I have tried most of the different combinations of measurements and have found only one to be fruitful in practice. This, illustrated in inserts A and B of figure 6, requires the measurement of elevation angle, the distance from the point of this measurement to a point under the bird's track, and information on the bird's track direction. It must also be assumed that the bird's track direction is reasonably constant during the relatively short period of time that the information is being obtained. This turns out to be a very reasonable assumption in practice, since the typical error in measuring the elevation angle affects the accuracy much more than uncertainty in the track.

Signal reflection from the ground causes very large errors in elevation angle measure-

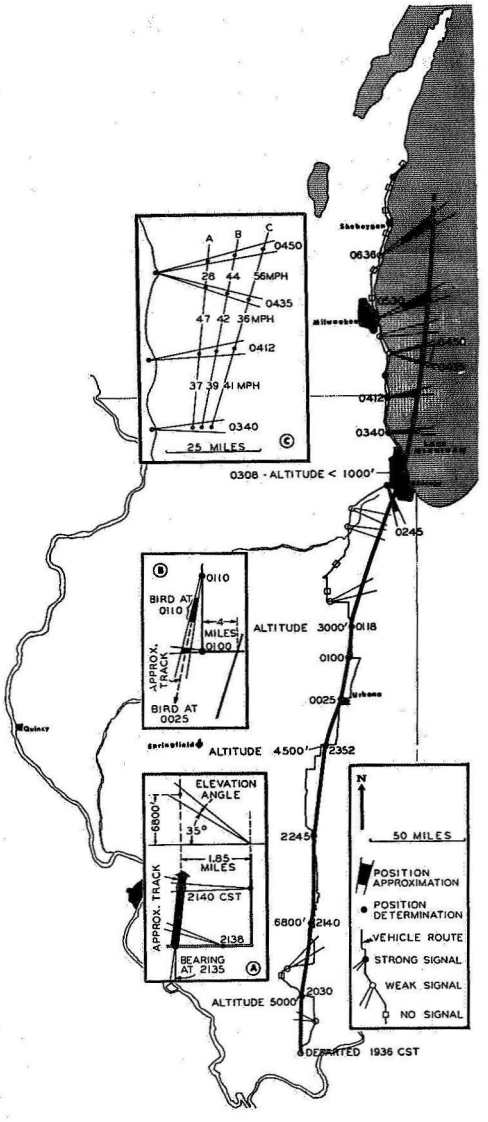


FIGURE 6. Flight of a veery, May 15, 1969. About one fourth of data gathered during flight is shown. Vehicle route diverged markedly from track after 2030 hours CST when we were lost and again shortly after 0118 hours CST to avoid passing through large towns and to take advantage of a four-lane highway. Inserts A and B show method used to determine altitude and position. Insert C shows how track over Lake Michigan was approximated (track B) by testing several tracks against the data.

ments below about 30°, and the method becomes very sensitive to errors in baseline measurement for elevation angles above about 60°. Also, cross-polarization makes the elevation angle difficult to measure when the tracking vehicle is in either of the two zones extending about 45° either side of the axis of the transmitting antenna. Therefore, it is desirable to be to the side of the bird and at a distance such that the elevation angle falls between 35° and 55°. To project where and when such conditions will occur relative to available primary roads and to be there at the right time is not as simple as it might appear in figure 6. The number of altitude determinations achieved in practice varies from about two per hour for a bird ground speed of 32 km/hr (20 mph) and numerous good roads to one or none in 6 hr for bird ground speeds above 64 km/hr (40 mph) and winding, less numerous, roads.

Although the method is valid regardless of the bird's altitude, difficulty in execution limits its use to altitudes above about 90 m. For example, a bird at an altitude of 30 m requires the positioning of the tracking vehicle about 30 m away for the period of 10 seconds or so that the bird is presenting a side aspect, then, in another 20 seconds or so moving the vehicle around 30 m to determine a cross-over position. That it usually takes some 15 seconds of rocking the antenna up and down to measure elevation angle is of itself sufficient to preclude such a feat, not to mention the difficulty in positioning the tracking vehicle. However, the rapid rate of change of signal strength and bearings as a bird moves in from a distance, passing within a few hundred meters, does at least dictate that the bird is very low. For altitudes between about 90 and 300 m, accuracy is quite poor (±30 percent) either because of the timing and positioning problems mentioned above or because a low elevation angle is involved as has been depicted in the insert in figure 9, page 53.

Determination of a bird's altitude by telemetry and while operating from an aircraft is accomplished by homing toward and past the bird at different altitudes. The homing run at which closest proximity to the bird is achieved is the one with an aircraft altitude that most closely matches that of the bird. Proximity is determined primarily by the rate of change in signal strength. When flying a path that passes within 75 m (250 ft) of a bird, the rate of change of distance is high; e.g., if the relative speed of approach is 60 m/sec (137 mph), starting at 900 m away, the range will halve to 450 m in 7.5 sec, to 225 m in another 4 sec, to 115 m in an additional 2 sec, and to closest point of approach in another 1.5 sec. Since halving distance increases the signal by a factor of 4, the signal increases very rapidly, especially during the last few seconds before closest approach. In practice, this is very obvious, almost terrifying as each successive beep dwarfs the preceding one giving one the impression of impending collision. If, however, the aircraft misses the bird by 225 m, the sequence starting at 900 m is to halve distance in about 8.2 sec and then to closest point of approach in the next 6.5 sec. This gives little more than a very noticeable increase in about 15 sec followed by a decreasing signal. Flying homing runs at altitude increments of 225 m seems to be a practical compromise between time consumed and accuracy, especially since there is no point in determining the bird's altitude more accurately than errors in winds-aloft measurements make meaningful. The method is of limited usefulness below about 150 m for flight safety reasons, especially at night. It is also unwise to use this method at night to determine the altitude of a large flock of whistling swans.

Because the method depends on proxim-

ity, large lateral errors in homing greatly reduce the rate of change of signal, even when flying at the same altitude as the bird. The side-looking yagi is neither accurate enough nor looking the right direction (ahead) for homing, but it is sufficient to establish the general direction from a considerable distance. For the last 2 km or so of approach, a different antenna system is needed. One simple system consists of two folded dipoles constructed from TV twin-lead and provided with coaxial cable baluns and equal-length coaxial cable leads. The two antennas are taped to the inside of the windows, one on each side, and placed as symmetrically as possible. A coaxial switch is used to switch the receiver back and forth between the left and right antennas. The procedure is to compare continually the signal amplitude obtained from each antenna and to maintain them nearly equal by instructing the pilot to alter the airplane heading. Because the axis of symmetry of an airplane is a vertical plane bisecting it fore-aft, and since the antennas are located off this plane of symmetry but equally so, the patterns of the antennas will be nonsymmetrically distorted and mirror image to each other. The asymmetry has been sufficient, in the several types of airplanes that I have used, to cause an easily detectable signal amplitude differential for deviations in the plane's heading of 5° from the true signal direction. Tests conducted on a transmitter in a tree gave consistent passes within a 60-m lateral error while flying at 90 m. Also, in using this method to follow a hawk migrating during the day, I found that about one-third of the closest passes resulted in a visual sighting of the bird within a few hundred meters.

The disadvantage of this method lies in the possibility that the observer will disturb the subject. This is especially pertinent during darkness when there is always the possibility that the airplane may force the bird to maneuver to avoid a real or imagined collision. Of the two dozen or so times I have used this method at night, there was only one passage close enough to have an observable result; the bird landed.

POSITION AND TRACK DETERMINATION

Positions are obtained by using various combinations of the measurements and estimates described above. A track is made up of a succession of positions. A position is an integral part of the geometric and proximity methods for altitude determination as described above.

A range estimate and bearing are sufficient to estimate position as for the numerous positional trapezoids of figures 6, 7, 8, and 9. Elapsed time coupled with track speed and direction measurements or estimates may also be used as with trapezoid *E F G H* of figure 9. A very accurate method requires maneuvering the tracking vehicle so that the bird will pass overhead. This is described and illustrated by Cochran et al. (ref. 3).

Another method requires two bearings spaced in time and from the same location, or several non-parallel bearings from different locations. These may be combined with approximate speed and track direction information to determine a best fit for the track segment or segments. Application of this method to position a bird over Lake Michigan is illustrated in insert C of figure 6 where track B is seen to be a better fit than A or C in regard to uniformity of ground speed.

ACCURACY

The accuracy of bearing measurements and range estimates under some of the variable conditions which occur has already been

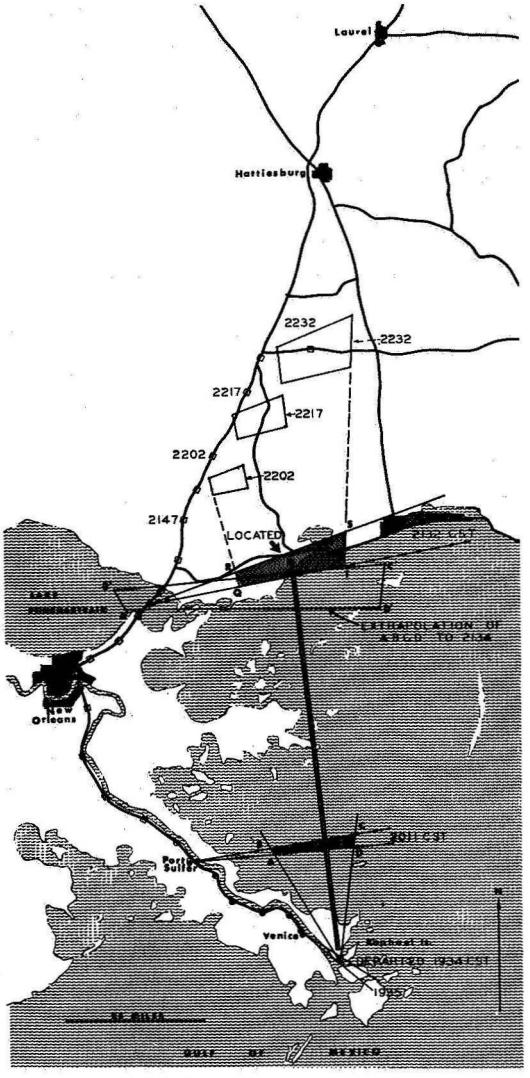


FIGURE 7. Flight of a veery from the Delta National Wildlife Refuge in May 1970. Key is same as in Figure 6.

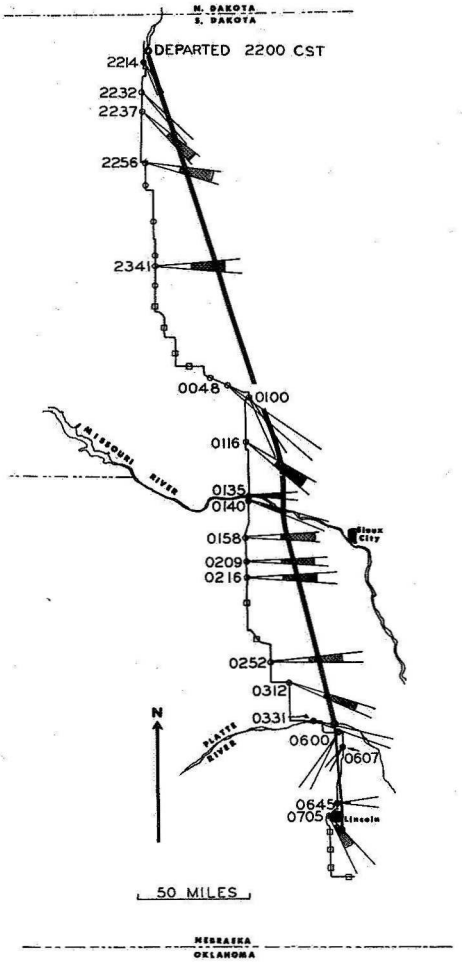


FIGURE 8. Flight of a radio-tagged goose (in a flock) in November 1967. Key is same as in Figure 6.

discussed. The word "estimate" has been substituted for measurement in discussing ranging by signal strength and fluctuation information since no numbered scale is used, but rather a judgment is made on the basis of past experience. Positioning, both altitudinal and map, involves calculations based on several measurements or estimates. The great variation in accuracy is evident from the difference between the positional approximations and determinations of figure 6.

From the standpoint of reporting results, especially where the results are used as arguments for or against a hypothesis, it is essential to discuss the accuracy of data to whatever extent such accuracy may affect the va-

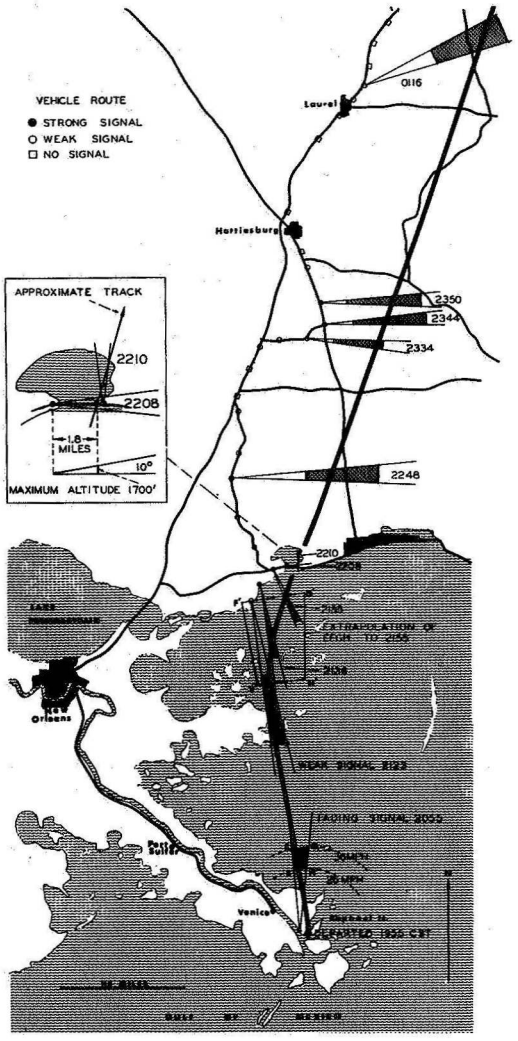


FIGURE 9 Flight of a gray-cheeked thrush in May 1970. Insert shows how position and altitude were determined at the bridge crossing the mouth of Bay St. Louis. No elevation angle was discernible indicating that it was less than 10°. The signal was not heard after 0116 hours CST and it was impossible to drive fast enough to be positioned on the extrapolated track further north. Key is same as in Figure 6.

lidity of the argument. In some cases positions are accurate enough that they may be plotted as points on a map with a scale of 12 or more km per cm without grossly misrepresenting their accuracy. Lines drawn between such points are inferred and must be regarded with caution. For example, four positions not lying on a straight line may be regarded in three ways. Three straight lines can be drawn between them showing a track change at the two middle points, two straight lines can be drawn showing a track change at their intersection, or a smooth curve drawn through them showing a gradual change in track. If a larger number of points is available and located such that they all fit a smooth curve but no three fit a straight line, then a smooth curve seems reasonable. If, however, they are located such that they fit two straight lines, then a track change at the intersection is probable although there is no way of knowing whether the change occurred in seconds or gradually over a longer period. Although the poorest position estimates determined by telemetry will plot as dots on a 30-cm (12-inch) globe, they must be represented as areas when a scale of about 12 km per cm is used. The greatest usefulness of position approximations is described below, but occasionally it is sufficient for an argument to be able to state that a bird was somewhere east of a given point at a particular time, etc.

The thick lines used in the figures to depict the tracks are shown only to clarify the technique and should be regarded accordingly. A careful examination of the relationships between the observations shown and the indicated tracks will be instructive in a way that cannot be fully described here.

TACTICS

Most of the methods and measurements required for obtaining a variety of flight information have been described above. A min-

imal objective in long-distance tracking is to locate the bird after each flight. Once a bird is airborne, the operational procedures observed in gathering flight information, interpreting this information and making decisions comprise tactics. Typical decisions to be made are which road to take from here, how fast to drive, when to take the time to get fuel, or make winds-aloft measurements, what area to search, whether to take a detour on a fast road and temporarily sacrifice contact or to proceed on a labyrinth of secondary roads in order to stay close, which bridge to take across a river, when to attempt an altitude determination, etc. For even a single flight, the possible combinations of decisions will number into the millions with thousands of these combinations potentially yielding success in regard to the minimal objective. Putting together a successful sequence of decisions that also maximizes the quantity of flight information gathered is more an art than a science. All information, including past experience with the particular bird or with the species, may need to be used in making decisions. Position estimates, although of limited usefulness as reportable data, are often the kind of information upon which better-than-random decisions are made. I have tracked many migrants without having to make other than the simplest decisions; however, these have been slow flights which happily coincided with good roads that enabled me to stay close. In tracking a bird over a long distance, the probability is low that such ideal conditions will prevail throughout.

STRATEGY

Because situations often arise where no tactical procedure can yield success, it is necessary to employ sound strategy to avoid these. To do this a careful overview of the situation is taken prior to the occurrence of a flight. When departure may occur, a variety of possible flight tracks, maximum probable speed of flight based on winds-aloft forecasts and bird capability, and whether some portion of the flight may occur over a large body of water or over mountainous terrain are considered in relation to road networks, average vehicle speed that might be confidently expected, proximity of an airport, and manpower available. These considerations result in decisions such as when to monitor and when to sleep, where to monitor from, whether to use an airplane or a vehicle, or both, etc. If funds were unlimited, one would always work with a comfortable redundancy of means; but such is not the usual case.

EXAMPLES

The number of examples available from 11 000 km (7000 mi) of bird tracking is almost endless so I shall pick from these only a few which will highlight some of the main tactical and strategic procedures.

One case of strategic error occurred when an early departure combined with a bit of tardiness resulted in the loss of a flight. Five days, including two night flights, brought a veery to a small woods about 6 km (4 mi) south of O'Hare International Airport northwest of Chicago. We drove to Chicago to monitor only on those days when the weather forecast indicated a chance for a flight. The relationship between weather and migration flights had been worked out from past flights and was highly predictable. The timing of departure in relation to sunset was also known from past flights but was not as predictable since flights had been initiated from 0.5 to 5 hr after sunset with most occurring from 1 to 3 hr after sunset. After 3 days, ideal weather conditions occurred. We arrived at the bird's location at sunset, took

winds-aloft measurements and decided that an airplane would not be needed since the 32 km/hr (20 mph) southeast winds greatly reduced the likelihood that the veery would fly toward Lake Michigan. Because windspeed plus bird airspeed could combine to give up to 72 km/hr (45 mph) groundspeed we decided to monitor from about 32 km (20 mi) north in order to provide a head start and to avoid the weekend Chicago area traffic. But before we could move to a new location, the veery took off. During the first hour we traveled only 24 km (15 mi) and were trailing the bird in the weak-signal area off its tail. Even so, we managed to maintain intermittent contact for an additional 2 hr. Had we arrived sooner we would have been in a more favorable starting position when the bird took off, although the bird might well have outdistanced us anyway. In retrospect, I feel that the correct strategy would have been to employ an airplane due to the strength of the favorable wind and to the decreasing suitability of roads as one travels further north in Wisconsin.

A veery flight (fig. 7) illustrates what can be done with very little information. The drive from Venice to the Lake Ponchartrain bridge north of New Orleans was timed at 2 hr during the time of evening that a flight could be expected. Even with an 8–16 km/hr tail wind, a bird would not be expected to cover the 110 km (70 mi) from Raphael Island to the Mississippi Coast in less than 2 hours. At the time of departure, the signal was at first weak, but within a minute it had become fairly strong indicating that the bird had attained at least several hundred feet of altitude. When we reached Port Sulphur, the signal was getting weak so we stopped to obtain an accurate bearing and estimated the range to be between 24 and 48 km (15 and 30 mi). From these the positional estimate bounded by trapezoid *ABCD* was made. This was extrapolated to 2 hr after take-off (*A'B'C'D'*) to give an idea of where to expect the bird when we reached the coastal area. The signal was heard as we crossed the Lake Ponchartrain bridge but then abruptly disappeared indicating that the bird had landed, but I could not be certain of this because our loss of altitude coming down the north side of the bridge may have caused the signal loss. On the basis of the new bearing and range estimate, another positional trapezoid was made (*QRST*) and this extrapolated northward in segments selected to provide for their cumulative coverage as we drove north. Since the signal was not heard again, it was concluded that the bird had landed somewhere south of these segments but north of or within QRST. The bird was later located as shown. The most important tactical decision made during this flight resulted in our continuing the chase after I was fairly certain the bird had landed. If I had immediately begun a search of QRST and if the bird had continued its flight, I would never have found it, whereas having assured myself that the flight did not continue still left ample time, that night and the following day, for searching.

Another flight from Raphael Island was that of a gray-cheeked thrush (fig. 9). Previous experience with this species in Illinois had shown it to be a slightly faster flyer than the veery and to have a tendency to fly headings from 350° to 010° and to select nights for migration with strong southerly winds. These factors dictated a different strategy. One person stayed at the Delta Waterfowl Refuge a few miles from Raphael Island to monitor for departure and to obtain a departure direction with a portable receiver. Shortly after the bird took off, he telephoned this information to Waveland, Mississippi, where the tracking vehicle was stationed. This provided ample time to make winds-

aloft measurements, and to decide whether to drive to an appropriate location to intercept the bird and plan a route, or, if the wind was very strong from the south, to pick up an airplane for which prior arrangements had been made. Had the track continued, even approximately, in the same direction after the bird reached land, the roads would have been quite adequate to follow the bird successfully. However, the inland winds aloft were stronger than and about 90° clockwise from the winds on the Gulf and caused the track to change to the east and the bird's ground speed to increase. These changes, coupled with poor roads to the northeast, enabled the bird to outdistance us and caused me to regret not having decided on using the airplane. I should point out here that I often tended to use the vehicle when, were it not for a very limited budget, I would have chosen an airplane.

The flight of a veery, illustrated in figure 6, is the longest flight recorded to date (about 740 km or 460 mi) and of the longest duration (at least 11 hr). This was completely unexpected on the basis of previous flights of this species. Therefore, the possibility for a flight over Lake Michigan was not even considered and no arrangements for an airplane were made. The increase in morning traffic, and our inability to remain awake caused us to lag behind so I have no idea whether the bird outdistanced us, fell in the lake, or flew out of range toward the east side of the lake. Because the vehicle route gave good coverage of the lake's west side for at least 80 km (50 mi) beyond the point where the signal was last heard and a thorough aerial search was made of the remaining 200 km (125 mi) of shore to the north, I am quite certain that the bird did not end up on the west shore.

The average ground speed of the bird was around 64 km/hr (40 mph) but excellent roads nearly paralleled the track over much of the flight; thus we were able to make numerous altitude measurements and occasionally afford the 10 min required to make winds-aloft measurements.

An interesting accessory was used to detect departure of the geese whose flight is shown in figure 8. A sensitive relay was connected to the receiver output and to the vehicle horn so that the horn blew whenever there was an increase in signal. If the threshold were properly set, the horn would blow only when the radio-tagged goose flew. The device proved effective for monitoring from distances up to 24 km (15 mi) from the geese. The goose departed on a migratory flight after about 2 weeks of our waiting and numerous false alarms due to local feeding flights. When the horn blew I was in bed and Mr. Kjos, the driver, was in the shower. Also, we had long since given up hurrying every time the horn blew. We got a very poor start on this flight. As can be seen in the figure, whenever we began to catch up in latitude we would be forced to go east and fall behind again. Nevertheless, we managed to maintain contact until the flock landed in the Platte River about 0334 hours CST. We placed the horn-alarm in operation and slept. At 0545 hours CST the alarm sounded and the chase was continued until the signal faded at 0705 hours CST. We proceeded as shown and, when no signal was heard along the extrapolated bird track, we back-tracked, conducting a search of the area of the position estimate of 0705 hours CST. The flock was located in a stubble field within an hour. Within another hour the transmitter failed, thereby thwarting the main objective which was to follow this bird to its wintering area in Oklahoma or Texas. Several points are of tactical interest. First, it was necessary to travel at top speed to keep up with the birds since they averaged over 95 km/hr (60 mph) groundspeed for most of the flight. Second, the only

two accurate positions for the first leg of the flight were the departure and landing points; at all other times estimates of position had to be used in deciding our route. At 0048 hours CST I had decided to cross the Missouri River at Sioux City, but the bearing obtained at 0100 hours caused me to change my mind and cross at Yankton. Had the track continued in a straight line either choice would have been equally bad, but the birds altered their heading about 0116 hours CST from 190° to 240° and maintained the new heading until they crossed the river. Note that the track shown is the resultant of the bird's heading and airspeed combined with winds. This brought their path closer to our route and also slowed their ground speed to about 72 km/hr (45 mph), enabling us to catch up temporarily. This was luck of course, not tactical genius. Lastly, somewhat analogously to the procedure taken in the veery flight shown in figure 7, I projected the track after I was reasonably certain that the bird had landed (at 0705 hours CST) and proceeded to cover this projected track, going back to search for the landed bird only after I was certain that the flight had not continued.

This flight is a prime example of how, in terms of long-distance tracking, half a flight is little better than none at all. From copious banding records I was reasonably confident that the objective for these geese was one of several refuge areas straight south of their departure point at Sand Lake, South Dakota. Their heading during the portion of the flight ending near Lincoln was straight south or slightly west of south. Yet their track, due to the strong west-northwest wind, was taking them considerably east of this alleged goal. The next 480–640 km (300–400 mi) of flight and 1 or 2 weeks of observation would have given information about how and when they corrected for the drift or indeed if they were intent on a goal to the east of those I suspected. Anyone who has given considerable thought to the difficulties in defining and observing wind drift can appreciate the severe depression that this 500-km (370-mi) half-flight caused us.

LONG-DISTANCE TRACKING

The usefulness of the track data for a bird migrating over a long distance is not self-evident. The flight data that has been gathered to date have, as Griffin predicted, enabled us to identify important factors influencing the timing and orientation of these flights. It is ironic that, having reached the technological point where I am confident that a thrush could be followed from Canada to South America, I am not certain that the data would add enough to what has already been found to justify the expense. I would also like to add that should anyone wish to do so for the sake of generating a glamorous press release in his name, he ought to do it with his own money.

However, assuming that such a feat would provide useful data on gray-checked thrush migration, I will describe briefly the strategy required. Several transmitters with predicted battery endurance of 30 days would be required. Every 15 to 20 days the bird should be re-captured, examined, and have its transmitter replaced. Periods with unfavorable weather for migration should be utilized for recapture to minimize the disturbance to the bird's migration.

A vehicle equipped for tracking, taking winds-aloft measurements, and communicating with aircraft would be required. An airplane should be used for every flight; a twin-engine aircraft should be used when over-water flights or above cloud-cover operations are anticipated. An instrument-rated pilot must be available for flights in bad weather. For the trans-gulf flight a U.S. Navy de-

stroyer would be ideal, but since this is out of the question, a multi-engine airplane would have to be used. Operating from a succession of nearest airport facilities, the airplane would be used to fly out to obtain a number of bird positions. The procedure would be repeated until the bird reached land.

The probability for success, barring a flight over Cuba, is very high. Of the 36 *Hylocichla* thrush flights I have traced with a vehicle, about half were completed to the landing point. Of the four thrushes followed with an airplane, two were located at the end of their flight. Thus, using only an airplane or vehicle for each flight, and assuming the percentages given above approximate probability, the probability of success for tracking a single bird for 10 flights would be one half to the tenth power or about .001. I feel that, had the techniques and equipment suggested above been used on all the birds I have followed, all would have been located after each flight. In fact, had only the expense for an aerial search for those birds lost been bearable, most would have been found. If the probability of success for each flight averages to 0.95 the chance for overall success for 10 flights is around 0.6. To have much of a chance for success in long-distance tracking, the technique must provide for a very high probability of success on each flight. This, coupled with the rapid accumulation of investment as the migration proceeds, dictates that a redundancy of means be employed. The situation is something like having to win 10 contests in a row; if the first is lost you can consider it practice, but if, after nine wins, the tenth is lost, it is a disaster.

ACKNOWLEDGMENTS

This work was supported by the National Science Foundation under Grants GB 3155 and GB 6680. I am especially grateful to Richard Graber who as co-principle investigator of GB 3155, was instrumental in initiating and carrying out the work in 1965; to Gene Montgomery, whose efforts were essential to the very successful spring of 1966; to Charles Kjos who has contributed to the study since 1967; and to the personnel of the Sand Lake and Delta National Wildlife Refuges for their hospitality and cooperation. My appreciation is extended to my wife for transmitter construction and field assistance; to George Swenson, Jr. for his piloting, encouragement and suggestions; to Mary Ann Kjos, Mrs. Juanita Tate, F. C. Bellrose, James Bailey, Robert Watson, Robert Phillips, George Swenson III, William Anderson, James Hughes, L. D. Mech, Jerry Pitts, Roger Applegate, John Moore and his wife, J. W. L. Sladen, Robert Rich and his wife, and Glen C. Sanderson for assistance in various phases of the study. I must also gratefully acknowledge the assistance of my sons, James and Bill and their friends Dave and Paul Morpurgo who, on numerous occasions when I could not find a driver, operated the equipment and took notes while I drove; they turned out to be excellent visual spotters when following pigeons and hawks.

DISCUSSION

WILLIAMS: How do you recapture radio-tagged birds?

COCHRAN: Different species may require different methods. Thrushes all seem to behave the same when they are stalked: they fly away. If a person moves slowly and does not create a great commotion the thrushes do not fly into the treetops but stay 10 or 20 m ahead and can occasionally be seen darting amidst the brush. They also travel in a circle, many times in fact, and it is only necessary to place one or two nets at places where they are seen to fly and to continue stalking until they complete the circle again—into a net. Stalking may be difficult in heavy underbrush with thorns, mud holes and so forth.

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Recent Statistical Methods for Orientation Data

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IN THE AREAS of animal orientation and navigation, directions are measured in various ways. Animals are either kept in cages and their movements or preferences with respect to a reference direction recorded, or they are released and at certain points of their path the bearings are measured. The purpose of a statistical analysis is to establish preferred directions and to compare them with geographical lines such as directions to breeding places, homeward directions, valleys, mountain ranges, shore lines, and the like. It is also important to find significant differences between experimental and control groups.

A comprehensive account of statistical methods in the analysis of directions for biologists was published in reference 1. In the past five years, there was considerable interest in this area by both theoretical and applied research workers. A host of new results and methods is available today.

This paper explains and illustrates those methods that are immediately useful for biologists. No attempt is made to review results that are of purely theoretical interest no matter how important they may be for future statistical research. We will restrict ourselves to the two-dimensional or circular case and omit the three-dimensional or spherical case.

An exhaustive bibliography is found at the end of this paper for the reader whose interest goes beyond the rather limited scope of this account. Only those publications are listed that are not already quoted in Batschelet, 1965 (ref. 1). Recent papers of basically mathematical interest can be found under such names as Ajne, Beran, Downs, Maag, Mardia, Rao, Schach, Stephens, and Watson. For the spherical case we refer the reader to Bingham (1964), Downs (1966, 1970), Downs and Gould (1967), Savary (1965), Selby (1964), Stephens (1967, 1969), Watson (1965, 1966, 1967, 1970).

NOTATIONS

We will use the same notations as in reference 1. Let $\alpha_1, \alpha_2, \cdots, \alpha_n$ be a *sample* of independent angles taken from a certain theoretical distribution. Without loss of generality we choose the positive x axis as zero direction and associate the positive sign with a counter-clockwise rotation (see fig. 1).

It is convenient to introduce unit vectors, that is, vectors of unit length pointing in the directions given by the angles α_i $(i = 1, \cdots, n)$. The tips of these unit vectors are located on the circumference of the unit circle.

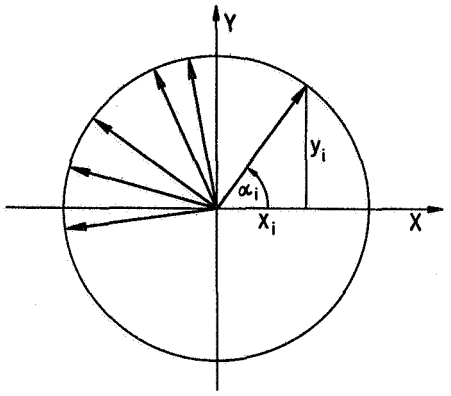

FIGURE 1. Circular sample represented by unit vectors.

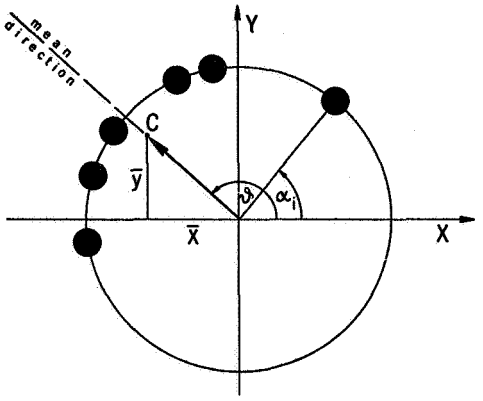

FIGURE 2. Circular sample represented by unit masses and their center C of gravity.

In a rectangular x,y-coordinate system the components of the unit vectors are

$$x_i = \cos \alpha_i,\ y_i = \sin \alpha_i \quad (i = 1, \cdots, n) \quad (1)$$

When a preferred direction or a mean direction is to be defined, we associate with each direction a unit mass which we locate at the tip of the corresponding unit vector (fig. 2). Then we calculate the coordinates of the center of gravity by

$$\bar{x} = \frac{1}{n} \Sigma x_i = \frac{1}{n} \Sigma \cos \alpha_i,\ \bar{y} = \frac{1}{n} \Sigma y_i = \frac{1}{n} \Sigma \sin \alpha_i \quad (2)$$

Denote the center of gravity by C. The vector which points to C is called the mean vector, whose components are x and y.

The length of the mean vector is denoted by r and may be calculated from

$$r = (\bar{x}^2 + \bar{y}^2)^{1/2} \quad (3)$$

An alternative way of calculating r uses vector addition. Consider again the unit vectors with components $\cos \alpha_i$, $\sin \alpha_i$ $(i = 1, \cdots, n)$. The sum of these vectors, also called the resultant vector, has components

$$V = \Sigma \cos \alpha_i,\ W = \Sigma \sin \alpha_i \quad (4)$$

The length of the resultant vector is

$$R = (V^2 + W^2)^{1/2} \quad (5)$$

Then the length r of the mean vector is simply

$$r = \frac{1}{n} R \quad (6)$$

If the population center of gravity falls into the origin, then no single preferred direction exists. This may be the case where all directions are equally likely, which is referred to as uniform distribution. Another possibility occurs with certain multi-modal distributions, for instance, when two opposite directions are equally probable.

We should also consider the influence of chance fluctuations. A sample may have a non-zero mean vector even if the underlying theoretical distribution has its center of gravity in the origin. It is therefore desirable to test whether r differs from zero significantly. Such tests will be presented in the following five sections.

Assume now that the length of the mean

vector is significantly different from zero and that the sample points are concentrated around a single preferred direction. Then we have good reason to introduce a mean direction, which is defined to be the direction of the mean vector. We denote its angle by ϑ (Greek theta) and call it the mean angle (fig. 2). This angle is calculated by solving the equations

$$x = r \cos \vartheta, \bar{y} = r \sin \vartheta \qquad (7)$$

or

$$V = R \cos \vartheta, W = R \sin \vartheta \qquad (8)$$

RAYLEIGH TEST AND MODIFICATION

The Rayleigh test is presented in reference 1, p. 28. For reasons that are explained there, the Rayleigh test should be used only in the unimodal case. The null hypothesis states that the theoretical distribution is uniform. As a test statistic we may use the length r of the mean vector. When r exceeds a certain critical value, the null hypothesis is rejected.

For the presentation of a table of critical values it is better to consider the test statistic

$$z = nr^2 \qquad (9)$$

instead of r itself. A short table of critical values adapted from work by Greenwood and Durand was published in reference 1. Now it is possible to enlarge this table (table 1) considerably by adapting tables published in reference 2 and by using an unpublished table kindly submitted by W. T. Keeton, Cornell University.

The Rayleigh test is most powerful if the alternative to the uniform distribution is a circular normal distribution (ref. 3).

Recently, a modification of the Rayleigh test has proved to be most useful.[1] It may occur that a particular direction is expected to be the preferred direction in advance of the experiment. For instance, when pigeons are released at a test site, the home direction is known in advance. The null hypothesis that we are going to test is randomness, which means that the angles of the sample are independent observations from a uniform circular distribution. For a test of the null hypothesis, it would be a loss of information when the knowledge of a predicted direction were abandoned. Indeed, by using this direction we obtain a more powerful test.

Let θ_0 be the angle of the predicted direction, and let R, ϑ be defined as above. When making the predicted directions to a new X-axis, then the X-component of R is

$$V' = R \cos (\vartheta - \theta_0) \qquad (10)$$

as shown in figure 3. By means of formula (8) we also get

$$V' = V \cos \theta_0 + W \sin \theta_0 \qquad (11)$$

which is more practical for numerical calculations.

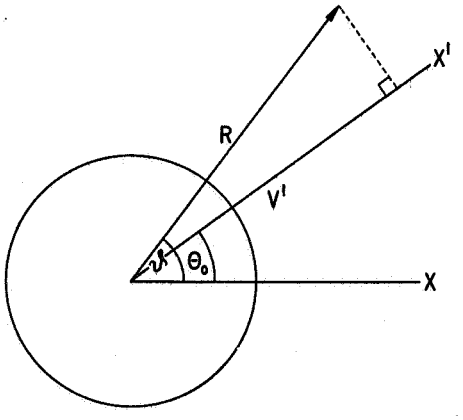

FIGURE 3. The V' component of R as used in the V test.

[1] I am indebted to Keeton for drawing my attention to the V test.

TABLE 1.—*Critical Values of the Test Statistic z of the Rayleigh Test*

n	P=10%	5%	2.5%	1%	0.1%
4	2.36	2.87	3.28	3.69	.....
5	2.29	2.84	3.34	3.86	4.91
6	2.29	2.86	3.40	4.08	5.30
7	2.29	2.88	3.45	4.16	5.56
8	2.29	2.90	3.48	4.20	5.74
9	2.29	2.91	3.50	4.25	5.88
10	2.29	2.92	3.52	4.29	6.00
11	2.29	2.93	3.54	4.32	6.06
12	2.29	2.93	3.55	4.34	6.16
13	2.29	2.94	3.57	4.36	6.22
14	2.29	2.94	3.58	4.38	6.27
15	2.29	2.95	3.59	4.40	6.32
16	2.29	2.95	3.59	4.41	6.35
17	2.29	2.95	3.60	4.42	6.39
18	2.29	2.95	3.60	4.43	6.42
19	2.29	2.96	3.61	4.44	6.45
20	2.30	2.96	3.61	4.45	6.47
21	2.30	2.96	3.61	4.46	6.49
22	2.30	2.96	3.61	4.46	6.51
23	2.30	2.96	3.62	4.47	6.53
24	2.30	2.96	3.63	4.48	6.54
25	2.30	2.97	3.63	4.48	6.56
30	2.30	2.97	3.64	4.49	6.62
35	2.30	2.97	3.64	4.51	6.66
40	2.30	2.98	3.65	4.52	6.69
45	2.30	2.98	3.65	4.53	6.72
50	2.30	2.98	3.66	4.54	6.74
∞	2.31	3.00	4.06	4.61	6.90

In an experiment of homing, V' denotes the so-called homeward component (ref. 1, p. 19), if θ_0 is the angle of the homeward direction.

The basic idea of the test is to consider the size of V'. If V' is small there is no evidence that the animals are oriented in the predicted direction with angle θ_0. If V' is relatively large, however, there must be some concentration of the directions around the predicted bearing. The larger the component V' is, the better chance there is of rejecting the null hypothesis of randomness. Therefore, we may choose V' as our test statistic. For this reason the test is called the V test (ref. 4).

The V *test leads to significance only if there is sufficient clustering around the predicted direction. In contrast the Rayleigh test is less powerful in this case but remains powerful for clustering on any part of the circle.*

For preparing a numerical table of criti-

TABLE 2.—*Critical Values of the Test Statistic* u *of the Modified Rayleigh Test* (V *Test*)

n	$P=0.10$	0.05	0.01	0.005	0.001	0.0001
5	$u=1.3051$	1.6524	2.2505	2.4459	2.7938	3.0825
6	1.3009	1.6509	2.2640	2.4695	2.8502	3.2114
7	1.2980	1.6499	2.2734	2.4858	2.8886	3.2970
8	1.2958	1.6492	2.2803	2.4978	2.9164	3.3578
9	1.2942	1.6486	2.2856	2.5070	2.9375	3.4034
10	1.2929	1.6482	2.2899	2.5143	2.9540	3.4387
11	1.2918	1.6479	2.2933	2.5201	2.9672	3.4669
12	1.2909	1.6476	2.2961	2.5250	2.9782	3.4899
13	1.2902	1.6474	2.2985	2.5290	2.9873	3.5091
14	1.2895	1.6472	2.3006	2.5325	2.9950	3.5253
15	1.2890	1.6470	2.3023	2.5355	3.0017	3.5392
16	1.2885	1.6469	2.3039	2.5381	3.0075	3.5512
17	1.2881	1.6467	2.3052	2.5404	3.0126	3.5617
18	1.2877	1.6466	2.3064	2.5424	3.0171	3.5710
19	1.2874	1.6465	2.3075	2.5442	3.0211	3.5792
20	1.2871	1.6464	2.3085	2.5458	3.0247	3.5866
21	1.2868	1.6464	2.3093	2.5473	3.0279	3.5932
22	1.2866	1.6463	2.3101	2.5486	3.0308	3.5992
23	1.2864	1.6462	2.3108	2.5498	3.0335	3.6047
24	1.2862	1.6462	2.3115	2.5509	3.0359	3.6096
25	1.2860	1.6461	2.3121	2.5519	3.0382	3.6142
26	1.2858	1.6461	2.3127	2.5529	3.0402	3.6184
27	1.2856	1.6460	2.3132	2.5538	3.0421	3.6223
28	1.2855	1.6460	2.3136	2.5546	3.0439	3.6258
29	1.2853	1.6459	2.3141	2.5553	3.0455	3.6292
30	1.2852	1.6459	2.3145	2.5560	3.0471	3.6323
40	1.2843	1.6456	2.3175	2.5610	3.0580	3.6545
50	1.2837	1.6455	2.3193	2.5640	3.0646	3.6677
60	1.2834	1.6454	2.3205	2.5660	3.0689	3.6764
70	1.2831	1.6453	2.3213	2.5674	3.0720	3.6826
100	1.2826	1.6452	2.3228	2.5699	3.0775	3.6936
500	1.2818	1.6449	2.3256	2.5747	3.0877	3.7140
1000	1.2817	1.6449	2.3260	2.5752	3.0890	3.7165

cal values, it is more practical to use the related test statistic

$$u = (2/n)^{1/2} V' \qquad (12)$$

A chart of critical values published in reference 4, p. 234, satisfies most practical purposes. The more accurate numerical table (table 2) was submitted by Keeton.

For applications of the V test see references 5 and 6. The following examples were also suggested by Keeton:

Example 1. Assume a random sample of directions as shown in figure 4. Despite an apparent clustering to the left, the Rayleigh test does not lead to significance ($z = 2.86$, $P > 0.5$). But when we learn that the home direction has azimuth $\theta_0 = 279°$, the prospect improves. Let us apply the V test. The azimuths α_i, listed in increasing order of magnitude, are 0°, 175°, 195°, 225°, 240°, 240°, 260°, 295°, 330°, 340°, and 345°. With $n = 11$ we get, from formulas (4), (5),

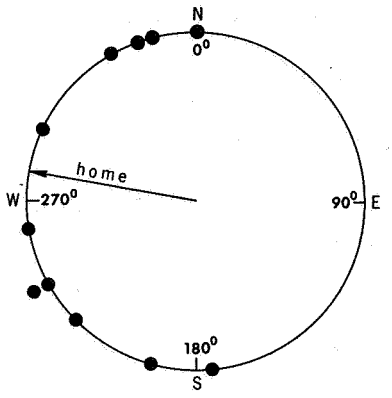

FIGURE 4. Home direction is used as predicted direction in application of V test.

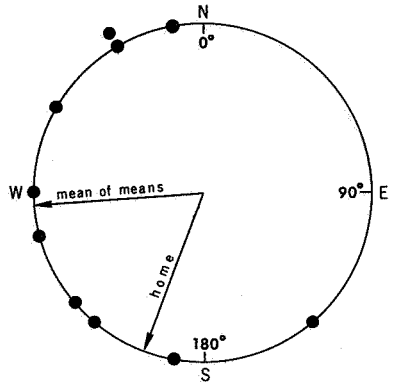

FIGURE 5. Long experienced mean direction serves as predicted direction in application of V test.

and (8), $V = +0.3514$, $W = -5.6026$, $R = 5.614$, and $\vartheta = 274°$. Then it follows from formulas (11) and (12) that $V' = +5.589$ and $u = 2.38$. For $n = 11$, table 2 reveals that $P < 0.01$. Hence the hypothesis of randomness can be rejected, whereas the Rayleigh test was too weak in our case.

Example 2. At a test site near Castor Hill, N. Y., it was observed in a long series of releases that the mean bearing of homing pigeons always deviated by roughly the same angle from the homeward direction. Figure 5 depicts the situation. The sample shown was collected under special experimental conditions that tend to increase the scatter of the bearings. The azimuths are 140°, 190°, 220°, 230°, 255°, 270°, 300°, 330°, 330°, and 350°. If we are interested in rejecting randomness, we may accept the long-experienced mean direction with azimuth $\theta_0 = 267.4°$ as a predicted direction. The test statistic of the V test is $u = 2.21$. Thus the V test leads to significance with a P value of less than 5 percent, whereas the Rayleigh test would fail again since P turns out to be nearly 10 percent ($z = 2.45$).

TEST BY HODGES AND AJNE

Hodges (ref. 7) proposed a bivariate sign test that later turned out to be quite useful in the analysis of directions.

Assume that two quantities are measured on each individual or experimental unit. Denote the two measurements by x and y and assume that the measurements are repeated n times. Thus we get the pairs

$$(x_i, y_i) \qquad i = 1, 2, \cdots, n$$

If the experiment is performed with the same individuals under different conditions, we get another sample consisting of n pairs, say

$$(x_i', y_i') \qquad i = 1, 2, \cdots, n$$

The null hypothesis states that the two samples were taken from the same bivariate distribution. To test this hypothesis we form the differences

$$x_i' - x_i, \; y_i' - y_i, \qquad i = 1, 2, \cdots, n$$

and plot these differences in a rectangular x, y-diagram. Thus we get n vectors with

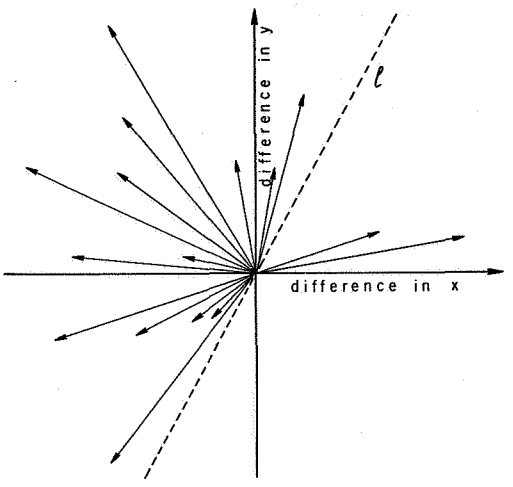

FIGURE 6. Hodges' test for paired bivariate samples.

components $x_i' - x_i$ and $y_i' - y_i$, respectively (fig. 6). If the null hypothesis is true, we would observe vectors pointing in all directions. If, on the other hand, the null hypothesis is wrong, the vectors should point to one sector of the x, y-diagram more frequently than to the rest of the plane.

To get a suitable test statistic we may draw a straight line l through the origin and count how many of the vectors point to one or the other side of l. Now we rotate l around the origin until we minimize the number of vectors on one side. This minimum is the test statistic. We denote it by K. If K is small enough compared with the sample size n, the null hypothesis can be rejected. Critical values for K can be found in table 3, which is adapted from tables in references 3 and 7. Hodges' test may be interpreted as an extension of the sign test to bivariate data.

Example 3. In figure 6 the sample size is $n = 16$, and the minimum number of vectors on one side of a straight line l is $K = 2$. The null hypothesis states that the measurements (x_i, y_i) and (x_i', y_i') belong to the same distribution.

Table 3 yields $P = 0.044$. Hence we can reject the null hypothesis at a 5-percent level of significance.

Example 4. In the paper in these proceedings entitled "Satellite and Ground Radio Tracking of Elk," F. C. Craighead et al. study the deviations between the actual location of an individual elk and the points tracked by a satellite. The errors of location are recorded as vectors in a horizontal plane in their figure 5.

Do the vectors indicate any preferred directions? Applying Hodges' test, we obtain $n = 17$ and $K = 6$. Table 3 yields a P-value greater than 0.500 or 50 percent. Hence we have no reason to assume a preferred direction.[2]

Notice, however, that east-west errors seem to be larger than north-south errors. To test significance of this kind we would need another test. Hodges' test is not sensitive to changes of variance.

Example 5. When tracking a single animal, a question frequently arises: Is the movement of the animal oriented or is it random? Consider figure 7 where the track of an animal is recorded. At a glance it appears that the animal is generally headed north and that it only occasionally deviates strongly from his course.

In the light of probability theory, the track may be considered as a realization of a stochastic process. It is very likely that consecutive sections of the track are dependent on each other. We want to show that the animal reorientates himself toward the north over and over again.

Present-day statistics is not able to

[2] I am indebted to C. E. Cote, Goddard Space Flight Center, Greenbelt, Md., for the permission to use his data.

TABLE 3.—*Critical Values of Test Statistics* K *in Relation to the Significance Level* P *and the Sample Size* n

n	$K=0$	1	2	3	4	5	6	7	8
8	$P=.063$	.375							
9	.035	.246							
10	.020	.156							
11	.011	.097	.376						
12	.006	.059	.258						
13	.003	.035	.171	.489			>.500		
14	.002	.021	.111	.355					
15	.001	.012	.070	.250					
16		.007	.044	.171	.444				
17		.004	.027	.114	.327				
18		.002	.016	.075	.233				
19		.001	.010	.048	.163	.399			
20			.006	.030	.111	.296			
21			.003	.019	.074	.213	.466		
22			.002	.012	.049	.151	.356		
23			.001	.007	.032	.104	.265		
24				.004	.020	.071	.193	.413	
25	<.001			.003	.013	.048	.137	.315	
26				.002	.008	.031	.096	.235	.466
27					.005	.020	.066	.172	.364
28					.003	.013	.045	.124	.278
29					.002	.008	.030	.087	.208
30					.001	.005	.020	.061	.153
35							.002	.008	.026
40									.003

prove that such a track is oriented. Nor is statistics able to deal with random walks. However, the following modest approach is possible: Let us play the role of a devil's advocate and assume that from time to time the animal chooses new directions "at random." The directions would be taken from a uniform circular distribution. We call this assumption the null hypothesis. We consider the points P_1, P_2, $\cdots$ reached by the animal at time 1 hour, 2 hours, $\cdots$, respectively, after release at P_0. (The time interval depends on the frequency of new decisions. In our example, we assume that a new decision is made at intervals smaller than an hour.) Now we form the vectors $\overrightarrow{P_0P_1}$, $\overrightarrow{P_1P_2}$, $\overrightarrow{P_2P_3}$, $\cdots$. Under the null hypothesis these vectors have random directions. We plot these vectors with a common base 0 and draw a line l that minimizes the number of vectors on one side of l. Applying Hodges' test to the vectors of our example, we get $n=13$, $K=1$. Table 3 yields $P=.035$. Hence we are able to reject the null hypothesis of randomness at a level of $P=5$ percent.

Ajne (ref. 3) proposes a circular one-

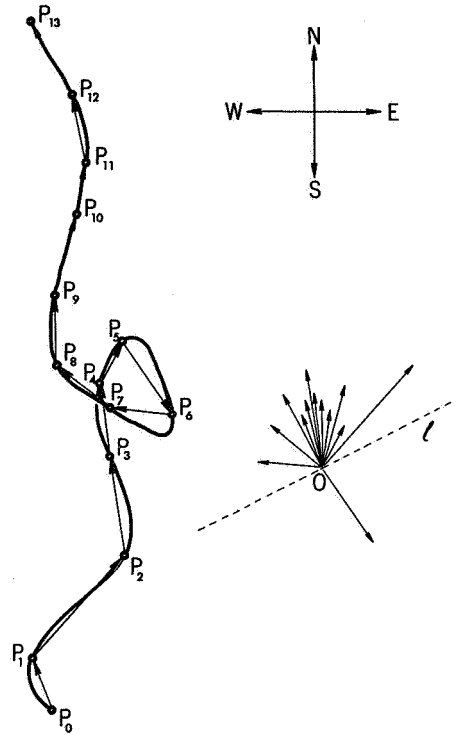

FIGURE 7. Track of an animal and a test for randomness.

sample test. The problem is the same as for the Rayleigh test discussed previously. Consider a sample from a unimodal circular distribution. Can a preferred direction be established statistically? The null hypothesis is a uniform distribution.

The test procedure is very simple once a circular plot is provided. We draw a straight line l through the center of the circle and count the number of sample points on each side of l. Then we rotate l and minimize the number of sample points on one side of l. This minimum number is denoted by K and used as a test statistic. If K is small relative to the sample size n, the null hypothesis of a uniform distribution is rejected.

We slightly modified the original formulation of Hodges' and Ajne's tests. Thus it becomes obvious that Ajne's test is a special case of Hodges' test. This connection was discovered by Bhattacharyya and Johnson (ref. 8). Ajne's test is powerful if the alternative to the uniform distribution is a rather narrow unimodal distribution (high degree of concentration around the mean direction).

Example 6. Homing pigeons were released singly. They disappeared at directions measured by the following azimuths (arranged in increasing order): 115°, 120°, 120°, 130°, 135°, 140°, 150°, 150°, 150°, 165°, 185°, 210°, 235°, 270°, and 345°. Sample size is $n = 15$. The line l can be drawn in such a way that the minimum number of sample points on one side of l is $K = 1$ (fig. 8). From table 3 we get $P = .012$. Hence the null hypothesis of a uniform distribution can be rejected at a 2-percent level of significance.

AJNE'S SECOND TEST

Ajne (ref. 3) proposes a further method for testing the null hypothesis of a uniform distribution. Consider again the straight line l in figure 8. If the theoretical distribution were uniform, we would expect an equal

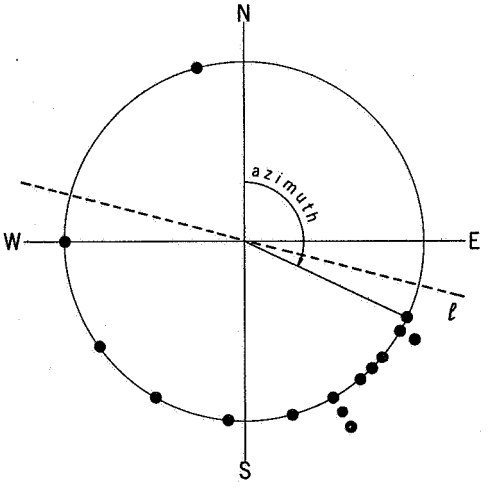

FIGURE 8. Ajne's test applied to an orientation problem.

TABLE 4.—*Critical Values for Ajne's Test Statistic* A *in Degrees*

n	P=10%	5%	2.5%	1%	0.5%
5	A=185	227	262	301	324
6	184	227	268	314	343
7	184	228	269	318	354
8	184	229	271	322	359
9	184	230	272	326	364
10	185	231	274	329	369
11	185	231	275	332	372
12	185	232	277	334	375
13	185	232	277	336	377
14	185	232	278	337	379
15	185	232	278	338	381
16	185	233	279	339	383
17	185	233	279	340	385
18	185	233	280	341	386
19	185	233	280	341	386
20	185	233	281	342	387
30	186	234	283	346	393
40	186	235	284	347	395
50	186	235	284	349	397
100	186	235	285	351	400
200	186	236	286	352	402
∞	185	236	287	354	404

number of sample points on each side of l, that is, $n/2$ sample points. A small deviation from $n/2$ may be due to chance fluctuation. A large deviation, however, indicates that the uniform distribution is not the proper hypothesis. When we rotate l around the center, the deviation from $n/2$ varies. Ajne chooses a suitably defined average of this deviation as a test statistic.

A rather lengthy mathematical analysis leads finally to the following procedure (ref. 9). Let $\alpha_1, \alpha_2, \cdots, \alpha_n$ be the observed angles in degrees and assume that they are arranged in ascending order. Thus

$$\alpha_1 \leqq \alpha_2 \leqq \alpha_3 \leqq \cdots \leqq \alpha_n \qquad (13)$$

Calculate the differences

$$m_{12} = \alpha_2 - \alpha_1,\ m_{13} = \alpha_3 - \alpha_1,$$
$$m_{23} = \alpha_3 - \alpha_2, \cdots$$

If one of them exceeds 180°, take the complementary value by subtracting it from 360°. For instance, if $\alpha_{10} - \alpha_1 = 205°$, take $m_{1,10} = 360° - 205° = 155°$. The differences may be arranged as follows:

$$\begin{array}{ccccccc} m_{12} & m_{13} & m_{14} & m_{15} & \cdots & m_{1,n} \\ & m_{23} & m_{24} & m_{25} & \cdots & m_{2,n} \\ & & m_{34} & m_{35} & & \vdots \\ & & & m_{45} & & \vdots \\ & & & & & m_{n-1,n} \end{array} \qquad (14)$$

Then form the sum of all these $n(n-1)/2$ differences, that is,

$$Z = \sum_{j=2}^{n} \sum_{i=1}^{j-1} m_{ij} \qquad (15)$$

With this sum the test statistic can be written in the form

$$A = n \cdot 90° - \frac{2}{n} Z. \qquad (16)$$

The null hypothesis of a uniform distribution is rejected if A exceeds a certain critical value. A table of critical values was published by Stephens (ref. 9); our table 4 is an adaptation of it.

Ajne's second test is especially powerful if the alternative to the uniform distribution is a unimodal distribution with a large angular deviation (low degree of concentration).

Example 7. We apply Ajne's test to the same data as in example 6. Here $\alpha_1 = 115°$, $\alpha_2 = 120°, \cdots, \alpha_{15} = 345°$. The differences in degrees arranged in the scheme (equation 14) are

5	5	15	20	25	35	35	35	• • •
	0	10	15	20	30	30	30	• • •
		10	15	20	30	30	30	• • •
			5	10	20	20	20	• • •
				5	15	15	15	• • •
					10	10	10	• • •
						0	0	• • •
							0	• • •

Notice that $\alpha_{15} - \alpha_1 = 345° - 115° = 230°$, but $m_{1,15} = 360° - 230° = 130°$. Formula (15) yields $Z = 6660°$. Hence, we get from formula (16)

$$A = 15(90°) - \frac{2}{15} 6660° = 462°$$

This value is larger than any critical value in table 4. Therefore, we can reject the null hypothesis of a uniform distribution at a 0.5-percent level of significance.

TEST BY LAUBSCHER AND RUDOLPH

Sometimes tests are required that are not necessarily powerful but are quick to apply. When testing uniformity versus a unimodal alternative on the circle, such a test could be quite useful. This was proposed by Laubscher and Rudolph (ref. 10) and also investigated by Rao (ref. 11).

Let R be the length of the smallest arc on the circle that contains all sample points. R may be called the range of the sample. A sufficiently small value of R indicates that the sample was not taken from a uniform distribution. Therefore, R can be chosen as a test statistic. If R is below a certain critical value, the null hypothesis of a uniform distribution can be rejected. A table of critical values follows (table 5) which is part of a table published in Laubscher and Rudolph (ref. 10).

Example 8. Six different migrating birds kept in cages moved toward average directions with the following azimuths: 122°, 93°, 158°, 67°, 85°, and 145°. Is the concentration of directions significant?

All six angles are between 67° and 158°. Hence the range is $R = 158° - 67° = 91°$. The critical value of R for a significance level of 1 percent is 100.2° (table 5). The sample range is below the critical value. Hence the null hypothesis of a uniform distribution can be rejected. The concentration of directions is indeed significant.

RAO'S TEST

The previous sections have dealt with the same topic—testing whether a circular sam-

TABLE 5.—*Critical Values n Degrees of the Range* R *of a Circular Sample*

n	*P*=.005	0.01	0.025	0.05	0.10
4	R=38.8	48.9	66.3	83.6	105.3
5	64.0	76.1	95.7	113.8	135.4
6	87.2	100.2	120.3	138.2	158.7
7	107.6	120.8	140.8	158.0	177.3
8	125.5	138.5	157.9	174.4	192.5
9	141.1	153.8	172.5	188.1	205.1
10	154.7	167.1	185.0	199.8	215.8
11	166.8	178.7	195.9	209.9	225.0
12	177.4	189.0	205.4	218.7	233.0
13	187.0	198.1	213.8	226.5	240.0
14	195.5	206.2	221.3	233.4	246.2
15	203.2	213.5	228.0	239.5	251.7
16	210.2	220.1	234.0	245.1	256.7
17	216.6	226.2	239.5	250.1	261.2
18	222.4	231.6	244.5	254.7	265.3
19	227.7	236.7	249.0	258.8	269.1
20	232.7	241.3	253.2	262.7	272.5
21	237.2	245.6	257.1	266.2	275.6
22	241.4	249.5	260.7	269.4	278.6
23	245.4	253.2	264.0	272.5	281.3
24	249.0	256.7	267.1	275.3	283.8
25	252.5	259.9	270.0	277.9	286.1
26	255.7	262.9	272.7	280.4	288.3
27	258.7	265.7	275.2	282.7	290.4
28	261.5	268.3	277.6	284.8	292.3
29	264.2	270.8	279.8	286.9	294.1
30	266.7	273.2	281.9	288.8	295.9

ple is taken from a uniform distribution. All of these tests are restricted to the situation where the alternative is a unimodal distribution.

However, multimodal distributions occur frequently in biology.[3] They have two or more preferred directions. When we apply one of the aforementioned tests to such data, the test loses most of its power; that is, it frequently fails to reject the null hypothesis of a uniform distribution even though the existence of modes is strongly suggested.

A test that is powerful in unimodal as well as multimodal situations was recently proposed by Rao (ref. 11). Its application is easy. Assume that the angles of a random sample are arranged in increasing order:

$$\alpha_1 \leqq \alpha_2 \leqq \alpha_3 \leqq \cdots \leqq \alpha_n$$

Then we calculate the length of all n arcs

[3] We will omit here the special treatment of multimodal distributions with strict symmetry.

TABLE 6.—*Critical Values for the Test Statistic* U *in Degrees*

n	$P=0.01$	0.05	0.10
4	U=221.0	186.5	171.7
5	212.0	183.6	168.8
6	206.0	180.7	166.3
7	202.7	177.8	164.9
8	198.4	175.7	163.4
9	195.1	173.5	162.4
10	192.2	172.1	161.3
11	189.7	170.3	160.2
12	187.6	169.2	159.2
13	185.8	167.8	158.4
14	184.0	166.7	157.7
15	182.2	165.6	157.0
16	180.7	164.9	156.6
17	179.6	164.2	155.9
18	178.2	163.1	155.2
19	177.1	162.4	154.8
20	176.0	161.6	154.4
25	171.9	158.9	152.7
30	168.8	156.7	151.4
35	166.4	155.0	150.3
40	164.4	153.6	149.5
45	162.7	152.4	148.7
50	161.2	151.4	148.1
100	152.8	146.8	143.7
200	146.8	142.6	140.4

between consecutive sample points on the circle. We denote these arc lengths by T_i.

$$\begin{aligned} T_1 &= \alpha_2 - \alpha_1, \\ T_2 &= \alpha_3 - \alpha_2, \\ &\cdots \\ T_{n-1} &= \alpha_n - \alpha_{n-1}, \\ T_n &= 360^\circ + \alpha_1 - \alpha_n \end{aligned} \qquad (17)$$

Notice that we always have

$$\Sigma\, T_i = 360^\circ \qquad (18)$$

If the theoretical distribution is uniform,

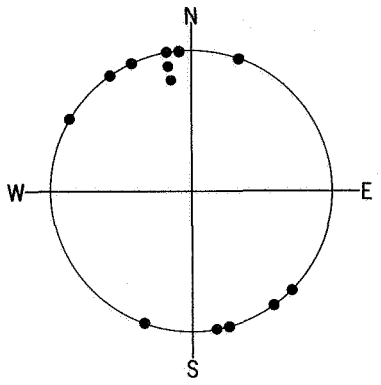

FIGURE 9. Testing a bimodal sample using Rao's test.

we expect that the T_i differ only slightly from each other. They fluctuate around their mean value $360^\circ/n$. On the other hand, if the T_i differ sufficiently from $360^\circ/n$, this indicates that the theoretical distribution is not uniform but rather unimodal or multimodal. Rao introduces the sum of deviations as test statistic; more specifically

$$U = \frac{1}{2} \sum_{i=1}^{n} \left| T_i - \frac{360^\circ}{n} \right| \qquad (19)$$

If U exceeds a certain critical value, the null hypothesis of a uniform distribution is rejected. The following (table 6) is a table of critical values for the U statistic. It is partly based on a table in reference 11.

Example 9. Homing pigeons were released singly in the Toggenburg Valley under subalpine conditions.[4] The birds did not adjust quickly to the homing direction but preferred to fly in the axis of the valley (fig. 9). The vanishing points are given by the angles arranged in ascending order: 20°, 135°, 145°, 165°, 170°, 200°, 300°, 325°, 335°, 350°, 350°, 350°, and 355°. Sample size is $n = 13$.

[4] I am indebted to G. Wagner, Bern, Switzerland, for the permission to use his data.

TABLE 7.—*Critical Values of the Test Statistic* $K = \sqrt{n}\,(D^+ + D^-)$

n	P=10%	5%	1%	0.1%
4	K=1.428	1.536	1.728	1.874
5	1.458	1.565	1.764	1.970
6	1.473	1.584	1.793	2.018
7	1.484	1.598	1.815	2.051
8	1.493	1.609	1.830	2.076
9	1.501	1.618	1.842	2.096
10	1.507	1.625	1.853	2.112
11	1.512	1.632	1.862	2.126
12	1.518	1.637	1.869	2.140
14	1.527	1.647	1.882	2.155
16	1.534	1.656	1.892	2.168
18	1.540	1.662	1.901	.....
20	1.546	1.665	1.908	.....
30	1.562	1.684	1.930	.....
40	1.571	1.695	1.941	.....
50	1.577	1.701	1.949	.....
60	1.582	1.705	1.955	.....
70	1.585	1.708	1.959	.....
80	1.588	1.711	1.962	.....
100	1.590	1.716	1.967	.....
∞	1.620	1.747	2.001	2.303

Does a uniform distribution fit these data? To test this possibility we apply Rao's U statistic. From formulas (17) we obtain

$$\begin{array}{lll} T_1 = 115^\circ & T_5 = 30^\circ & T_9 = 15^\circ \\ T_2 = 10^\circ & T_6 = 100^\circ & T_{10} = 0^\circ \\ T_3 = 20^\circ & T_7 = 25^\circ & T_{11} = 0^\circ \\ T_4 = 5^\circ & T_8 = 10^\circ & T_{12} = 5^\circ \\ & & T_{13} = 25^\circ \end{array}$$

As a check of computation we get $\Sigma T_i = 360^\circ$.

Since $360^\circ/n = 27.7^\circ$, we obtain from formula (19)

$$U = \frac{1}{2}(87.3 + 17.7 + 7.7 + 22.7 + 2.3 + 72.3 + 2.7 + 17.7 + 12.7 + 27.7 + 27.7 + 22.7 + 2.7) = 162^\circ$$

For $P = 0.05$ we get from table 6 the critical value 167.8°; our U value from the sample is somewhat below this. Thus we were not able to establish significance at a 5-percent level. However, a slightly higher sample size, say $n = 15$, would probably have yielded the desired result.

KUIPER'S GOODNESS-OF-FIT TEST

In reference 1, Kuiper's test was described in detail. The test could serve the same purpose as the previous tests, that is, to decide if a circular distribution is uniform.

Stephens (ref. 12, table 1) slightly corrected the table of critical values for the test statistic and enlarged it considerably. Table 7 is based on Stephens' findings.

Kuiper's test can be used in the unimodal and the multimodal case. A test related to Kuiper's test is Watson's U^2 test. It is described in reference 1 (p. 27). In samples occurring in biology, Watson's test is at least as powerful as Kuiper's test.

Example 10. We apply Kuiper's test to the data of example 9. Following the test procedure as explained in reference 1, p. 26, we obtain figure 10. From this figure we read

$D^+ = .023$ and $D^- = .369$. Hence

$$K = \sqrt{n}(D^+ + D^-) = \sqrt{13}(.023 + .369) = 1.414$$

From table 7 we obtain the critical value $K = 1.642$ at a 5-percent level of significance.

Our K value from the sample is smaller. Therefore, we cannot claim a significant deviation from the uniform distribution. The result is consistent with our findings based on Rao's test.

CONFIDENCE INTERVALS FOR THE MEAN ANGLE

In the case of a unimodal distribution, it is convenient to work under the hypothesis of circular normal distribution introduced by von Mises in 1918. The probability density function is

$$f(\alpha) = Ce^{\kappa(\alpha-\theta)} \qquad (20)$$

where θ denotes the mean angle, κ the parameter of concentration, and C a numerical constant depending on κ. More details, charts, and tables are given in reference 1.

If we are given a sample of n independent angles $\alpha_1, \alpha_2, \cdots, \alpha_n$, it is often demanded to estimate the parameters θ and κ. As a point estimate of θ, we take the mean angle ϑ calculated from the sample (formula 7).

In addition, the research worker wants to know the reliability of this estimate. The

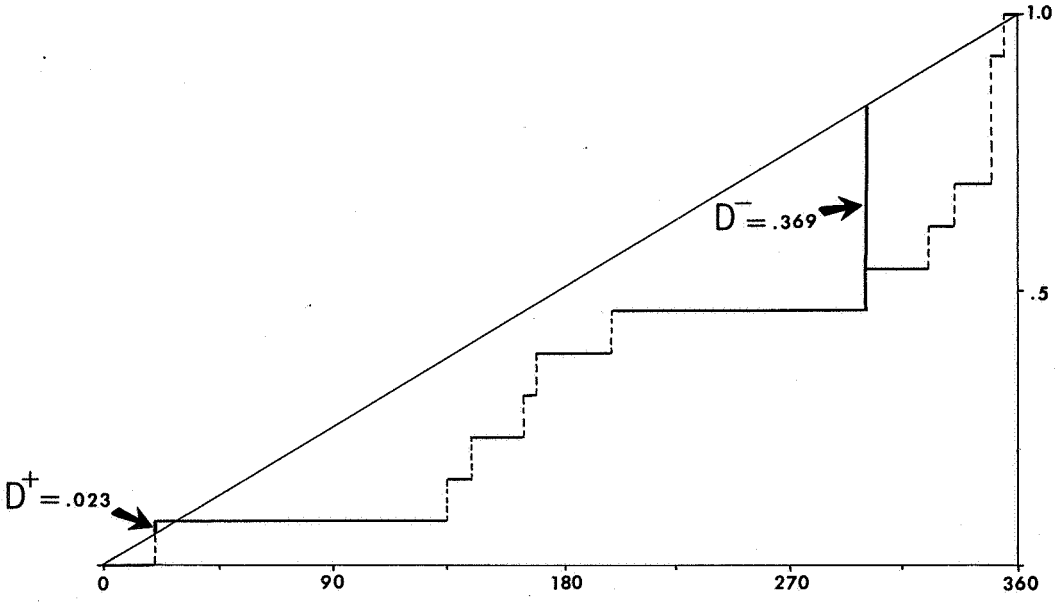

FIGURE 10. Application of Kuiper's test to a circular sample.

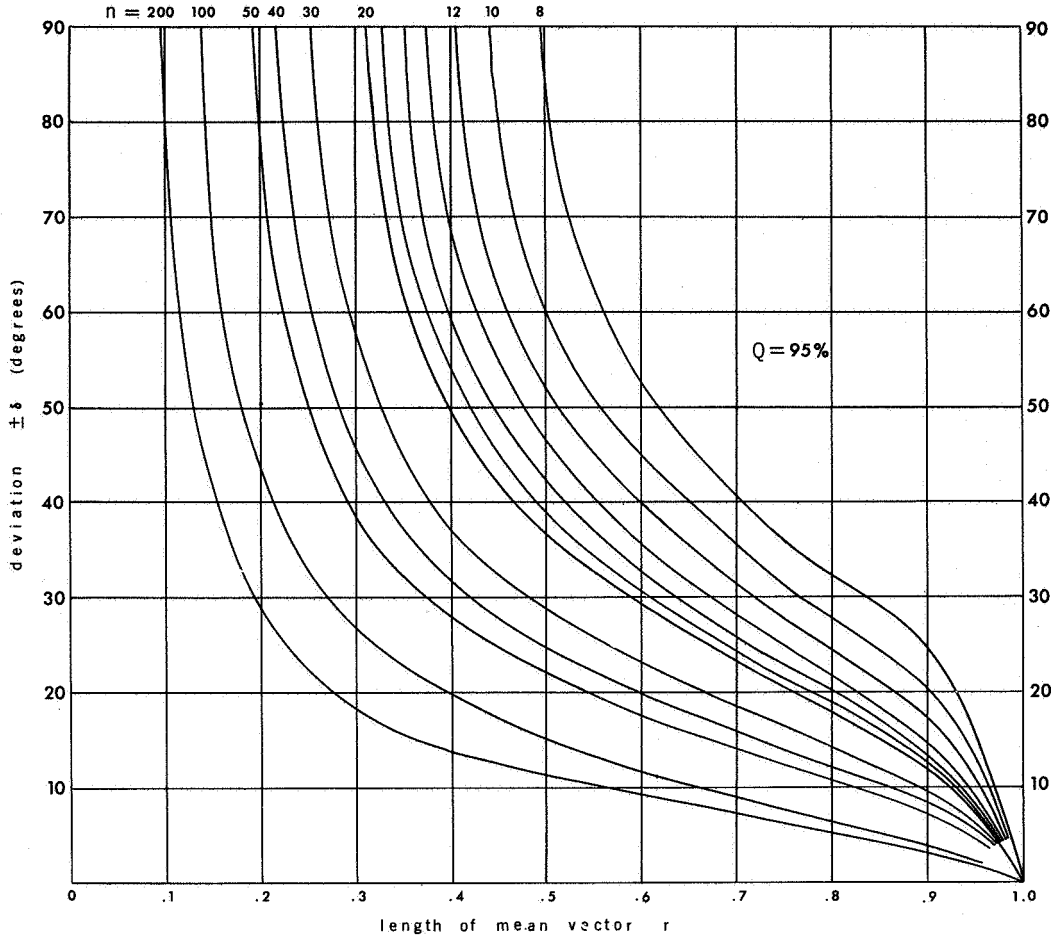

FIGURE 11. Chart for determining a confidence interval of the mean angle with a 95 percent confidence coefficient.

question is then to find an interval around ϑ in which the unknown parameter θ falls with a preassigned probability Q, called the confidence coefficient.

In reference 1 a confidence interval of the form

$$\vartheta \pm \delta \qquad (21)$$

was presented. However, the method to determine the deviation δ is somewhat sophisticated. It was therefore a good idea (ref. 13) to search for a direct graphical approach. Brown and Mewaldt present a chart from which the deviaton δ can be read as a function of the sample size n and the length r of the mean vector. Their chart was prepared for only $Q = 99$ percent and is fairly sketchy. It seemed worthwhile to follow their idea and to draw accurate charts. Figures 11 and 12 yield δ for confidence coefficients $Q = 95$ percent and $Q = 99$ percent, respectively.

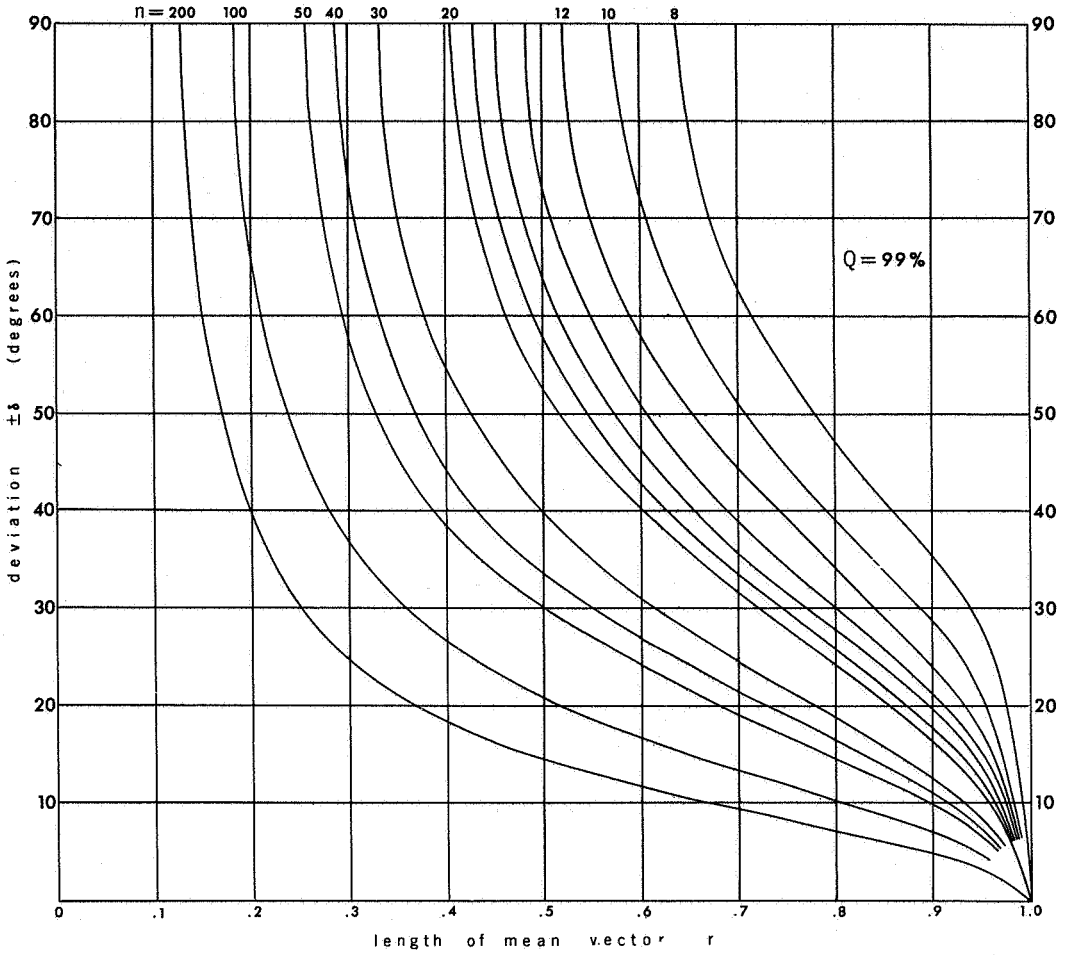

FIGURE 12. Chart for determining a confidence interval of the mean angle with a 99 percent confidence coefficient.

Example 11. In example 6 the null hypothesis of a uniform distribution was rejected. It is reasonable to assume that the sample was taken from a circular normal distribution with unknown mean angle θ and unknown parameter κ of concentration.

To estimate θ we first determine the center of gravity following the instructions given in the second section of this paper. We get

$$\Sigma \cos \alpha_i = -8.5723,$$

$$\bar{x} = \frac{1}{15}(-8.5723) = -.5715,$$

$$\Sigma \sin \alpha_i = +3.8478,$$

$$\bar{y} = \frac{1}{15}(3.8478) = +.2565,$$

$$r = (\bar{x}^2 + \bar{y}^2)^{1/2} = .6264,$$

$$\cos \vartheta = \frac{x}{r} = -.9123,$$

$$\sin \vartheta = \frac{y}{r} = +.4095,$$

$$\vartheta = 155.8°$$

Now we choose $Q = 95$ percent as con-

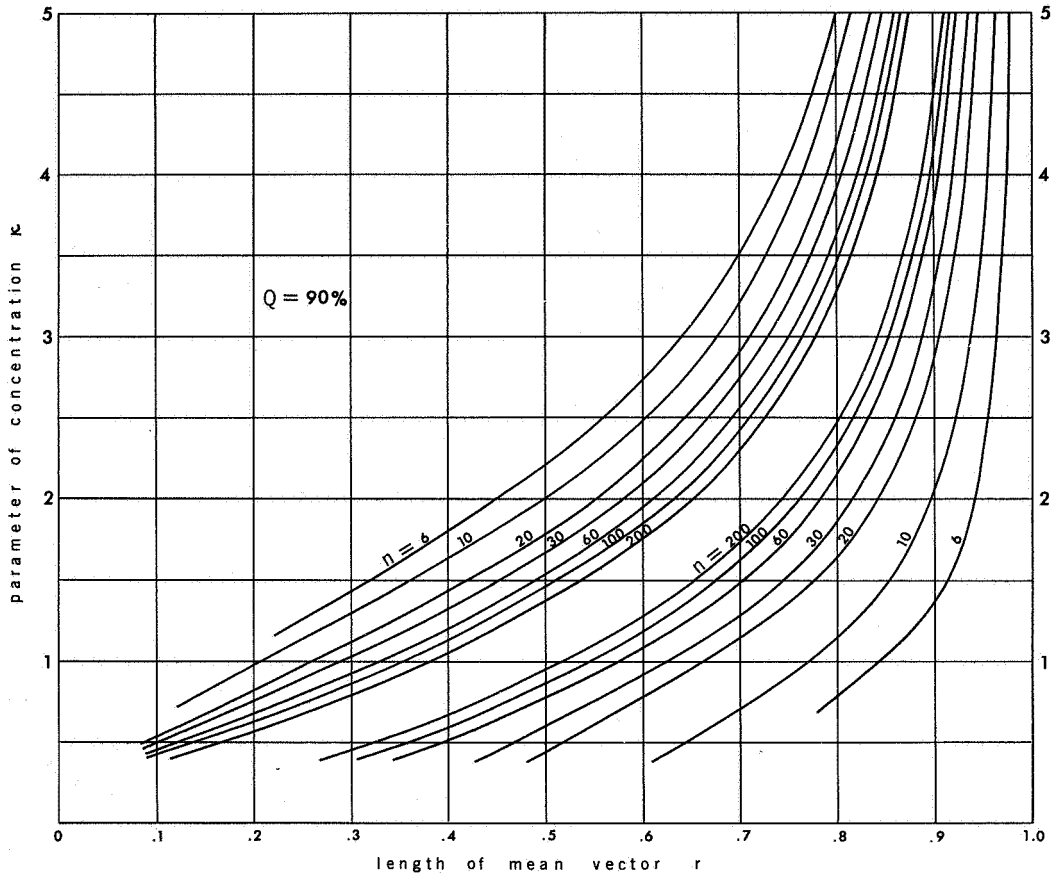

FIGURE 13. Chart for determining a confidence interval of the parameter of concentration with a 90 percent confidence coefficient.

fidence coefficient. In figure 11 we find lines for sample sizes $n = 14$ and 16. Our sample size is $n = 15$ so that we have to interpolate. At $r = .6264$ we find $\delta = 30.6°$ for $n = 16$ and $\delta = 33.4°$ for $n = 14$. Hence $\delta = 32.0°$ fits our purpose. Using formula (21) our confidence interval for θ turns out to be

$$155.8° \pm 32.0°$$

CONFIDENCE INTERVALS FOR PARAMETER OF CONCENTRATION

As in the previous section, we assume that the theoretical distribution is a circular normal distribution with probability density function (20). Our purpose is to estimate the parameter κ.

Values of κ range from 0 to ∞. The particular value $\kappa = 0$ indicates that the distribution is uniform. The higher the value of κ, the stronger is the concentration about the mean direction. Usually κ has to be estimated when the mean angle θ is unknown. The estimation is based on the length r of the mean vector, which was defined in formula (3). For a point estimate of κ, we use table B in the appendix of reference 1.

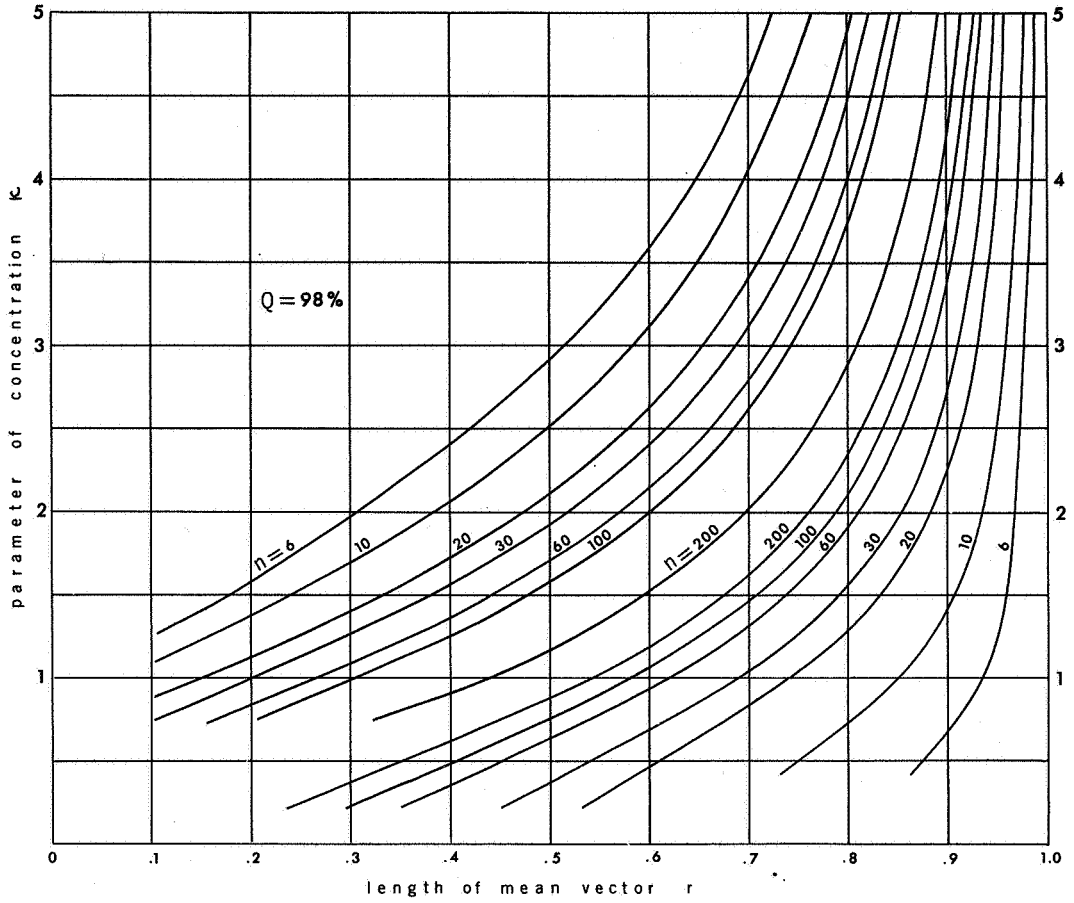

FIGURE 14. Chart for determining a confidence interval of the parameter of concentration with a 98 percent confidence coefficient.

There r ranges from 0 to 1 in steps of 0.01. The estimate of κ can be read in the third column.

Stephens (ref. 14) studied the theoretical distribution of r for a variety of circular normal distributions where κ ranges from 0 to 5. Based on his table 2, the following charts were drawn: Figures 13 and 14 give upper and lower confidence limits for κ for various sample sizes n and for the confidence coefficients $Q = 90$ and 98 percent, respectively. The use of the charts is explained in example 12.

We denote the lower limit by κ_l and the upper limit by κ_u. Thus the confidence interval is

$$\kappa_l < \kappa < \kappa_u \qquad (22)$$

Notice that sometimes the lower confidence limit is zero so that there is no uncertainty on the lower side of the interval. In this case the confidence coefficient has to be raised approximately from 90 to 95 percent and from 98 to 99 percent, respectively.

Example 12. We return to example 11.

There $n = 15$ and $r = .6264$. To get a point estimate of κ, we use table B in the appendix of reference 1. For $r = .62$ we find $\kappa = 1.60044$. For $r = .6264$ we get by linear interpolation $\kappa = 1.629$.

For confidence limits of κ, we choose $Q = 90$ percent as our confidence coefficient. In figure 13 we find curves for $n = 10$ and $n = 20$. For our own sample with $n = 15$ we will have to interpolate. For the lower limit we read from the lower curves at $r = .6264$

$$n = 10, \qquad \kappa_l = 0.44,$$
$$n = 20, \qquad \kappa_l = 0.88.$$

By linear interpolation for $n = 15$ we obtain

$$\kappa_l = 0.66$$

Similarly for the upper limit we read from the upper curves at $r = .6264$

$$n = 10, \qquad \kappa_u = 2.62,$$
$$n = 20, \qquad \kappa_u = 2.40.$$

Linear interpolation for $n = 15$ leads to

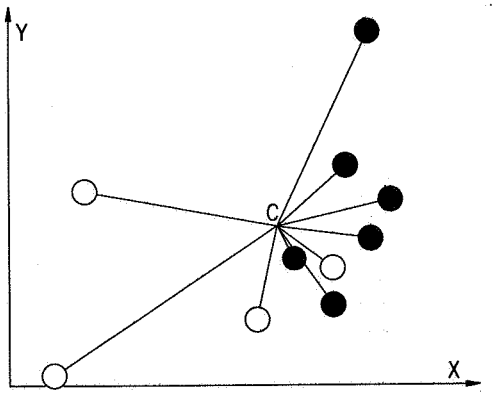

FIGURE 15. Testing two bivariate samples. One sample is represented by open circles, the other sample by filled circles. (Mardia's test).

$$\kappa_u = 2.51$$

Hence with probability 90 percent we conclude that

$$0.66 < \kappa < 2.51$$

Notice that the point estimate $\kappa = 1.629$ does not fall exactly into the center of this interval.

TWO-SAMPLE TEST BY MARDIA, WATSON, AND WHEELER

Wheeler and Watson (ref. 15) proposed a test procedure for comparing two circular samples. This test is nonparametric and powerful; for both reasons the test should be favored by research workers.

Mardia (ref. 16) has shown that Watson's and Wheeler's test is a special case of a bivariate test proposed by Mardia (ref. 17). Mardia also provided tables of critical values for the test statistic. Therefore, it seems to be appropriate to attribute the circular test to all three authors and to name it the Mardia-Watson-Wheeler test. In this section we will first explain Mardia's bivariate test and later consider the special case for circular samples.

We consider a sample of bivariate observations

$$(x_i, y_i), \qquad i = 1, \cdots, m.$$

and a second sample

$$(x_j', y_j'), \qquad j = 1, \cdots, n.$$

We want to know whether the two samples belong to the same bivariate population. To explain the test procedure we plot the sample points (fig. 15). The sample points (x_i, y_i)

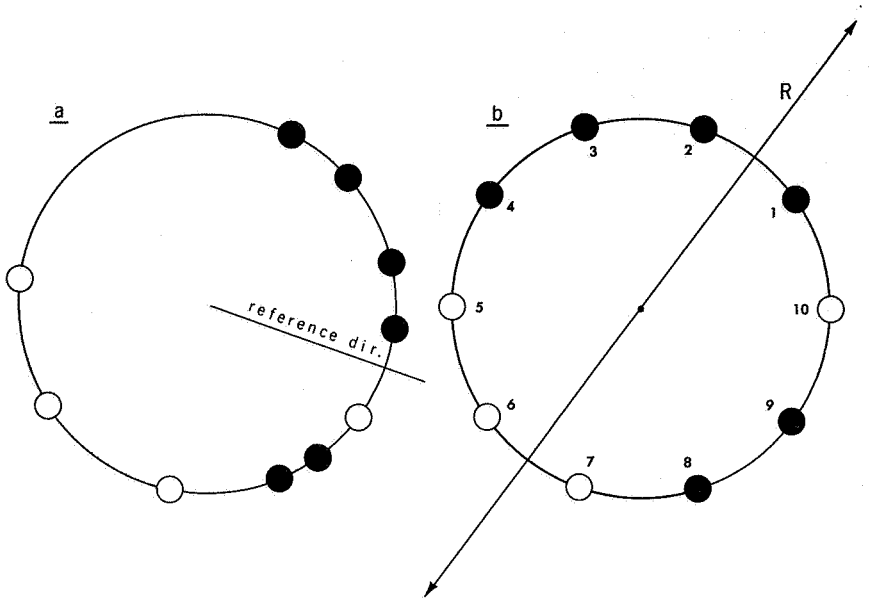

FIGURE 16. (a) Reduction of bivariate samples to circular samples. (b) Generation of equidistant sample points (Mardia-Watson-Wheeler test).

of the first sample are plotted by filled circles and the sample points (x_i', y_i') of the second sample by open circles. The second sample is located slightly to the left and below the first sample. Is this shift due to chance only or were the samples drawn from different populations?

To find a statistical answer to this question we pool the two samples and calculate the coordinates of the common center C of gravity using the formulas

$$\bar{x} = \frac{\Sigma x_i + \Sigma x_j'}{m+n}, \quad \bar{y} = \frac{\Sigma y_i + \Sigma y_j'}{m+n} \tag{23}$$

The center C of gravity is marked in figure 15.

From C we draw vectors to all $m + n$ sample points and consider their directions. Mardia's test is based on these directions only; thus the test reduces the bivariate case to the circular case (fig. 16a).

Now we rank the $m + n$ directions with numbers 1, 2, 3, $\cdots$, $m + n$ by starting at any reference direction and by rotating counterclockwise. Let

$$r_1, r_2, \cdots, r_m$$

be the ranks of the first sample, and

$$r_1', r_2', \cdots, r_n'$$

the ranks of the second sample. In figure 16a we see that $r_1 = 1$, $r_2 = 2$, $r_3 = 3$, $r_4 = 4$, $r_5 = 8$, $r_6 = 9$ and $r_1' = 5$, $r_2' = 6$, $r_3' = 7$, $r_4' = 10$. We have tacitly assumed that there are no intersample ties.

As a next step we introduce $n + m$ equally spaced dots on the circumference of the unit circle and mark them in the same order as the dots of the original samples (fig. 16b). If the dots of one sample are sufficiently separated from the dots of the other sample,

we conclude a significant difference between the samples. To define a test statistic we concentrate on one of the two samples. The choice is irrelevant. Then we calculate the length R of the resultant vector using formulas (4) and (5). When choosing the first sample, the angles are

$$\beta_i = \frac{360°}{n+m} \cdot r_i \qquad i = 1, 2, \cdots, m \quad (24)$$

Hence

$$V = \sum_{i=1}^{m} \cos \beta_i, \; W = \sum_{i=1}^{m} \sin \beta_i,$$
$$R = (V^2 + W^2)^{1/2} \quad (25)$$

In figure 16b the angles β_i are plotted with the horizontal direction as zero line:

$$\beta_1 = 36°, \quad \beta_2 = 72°, \quad \beta_3 = 108°,$$
$$\beta_4 = 144°, \quad \beta_5 = 288°, \quad \beta_6 = 324°$$

Hence $V = 1.118$, $W = 1.539$, $R = 1.902$.

This length R can be used as a test statistic. If R is sufficiently large, the dots of the first sample are concentrated around a preferred direction and thus more or less separated from the dots of the second sample. This argument is very similar to the procedure of the Rayleigh test (see the third section). Thus, in a certain sense, the two-sample test is reduced to a one-sample test, an idea which was successfully applied to other tests (ref. 18).

Instead of R itself, Mardia uses the following function of R as a test statistic

$$B = R^2 \quad (26)$$

If B exceeds a certain critical value, we reject the null hypothesis that the samples were taken from the same population.

The Mardia-Watson-Wheeler test can be safely used only if there are no intersample ties, that is, if no angle of the first sample coincides with an angle of the second sample. When the test leads to significance, this does not necessarily imply that the two samples differ in location. It could well occur that the main reason for significance is a difference in dispersion. This property is typical for most nonparametric tests. For a discussion see reference 1 (p. 34, especially figure 23.1).

Table 8 of B values is based on table 1 of reference 17.

For $N > 17$, Mardia (ref. 17) gives the following approximate distribution:

The quantity

$$U = \frac{2(m+n-1)}{m\,n} R^2 \quad (27)$$

is approximately distributed as χ^2 with two degrees of freedom. Using a table of critical χ^2 values, it is easy to find critical values for U.

In our illustrative example of figures 15 and 16 we got $R = 1.902$. Hence, $B = R^2 = 3.62$. For $n + m = N = 10$ and $n = 4$, the critical value is 9.47 at a 5 percent level of significance. Our B value is smaller. Thus we cannot claim significance.

For a biological example see Mardia (ref. 16, p. 189).

WATSON'S U^2 TEST

A nonparametric two-sample test attributed to Cramér, von Mises, and Smirnov was adapted for the circular case by G. S. Watson. The test was explained and exemplified in reference 1 (pp. 35 and 36). The test statistic is denoted by $U^2_{n,\,m}$ where n and m are the two sample sizes.

The lack of critical values of $U^2_{n,\,m}$ has prohibited the use of this test in the beginning. Now tables of critical values are avail-

TABLE 8.—*Critical Values of the Test Statistic* B. *(The Two Samples Are of Size* m *and* n, $m \geqq n$, $N = m + n$.)

N	n	P=0.001	0.01	0.05	0.10
8	4				6.83
9	3				6.41
	4				4.88
10	3				4.62
	4			9.47	6.24
	5			10.47	6.85
11	3				5.23
	4			10.42	7.43
	5			12.34	6.60
12	3			7.46	5.73
	4			9.71	7.46
	5		13.93	10.46	7.46
	6		14.93	11.20	7.46
13	3			7.68	6.15
	4			9.35	7.03
	5		15.26	10.15	7.39
	6		17.31	10.42	8.04
14	3			7.85	6.49
	4		12.34	9.30	7.60
	5		15.44	10.30	7.85
	6		15.59	12.21	7.94
	7		16.39	11.65	8.85
15	3				6.78
	4		12.78	8.74	7.91
	5		14.52	10.36	7.91
	6		17.48	11.61	9.12
	7	22.88	16.14	11.57	9.03
16	3			7.81	5.83
	4		13.14	9.44	7.38
	5		15.55	10.44	9.03
	6	22.43	16.98	11.54	9.11
	7	25.27	18.16	12.66	9.78
	8	26.27	18.89	13.14	9.44
17	3			8.01	6.14
	4		13.10	9.74	7.64
	5	18.86	16.44	11.03	8.76
	6	23.73	17.76	12.21	9.41
	7	27.40	17.98	12.63	10.11
	8	29.37	19.11	13.36	10.15

TABLE 9.—*Critical Values for Watson's* $U^2_{n,m}$. *(The Two Samples Are of Sizes* n *and* m,n $\geqq$ m)

n,m	*P*=10%	5%	1%	0.1%	*n,m*	*P*=10%	5%	1%	0.5%
10, 6	.153	.182	.243	.266	20, 4	.151	.178	.231	.251
10, 7	.153	.183	.246	.270	20, 6	.152	.182	.245	.270
10, 8	.153	.183	.248	.273	20, 8	.152	.183	.251	.278
10, 9	.153	.184	.249	.275	20, 12	.153	.185	.256	.285
10, 10	.153	.184	.250	.277	20, 16	.153	.185	.258	.289
12, 6	.153	.182	.244	.268	20, 20	.153	.185	.259	.290
12, 7	.153	.183	.247	.272	25, 5	.151	.180	.240	.263
12, 8	.153	.184	.249	.275	25, 10	.152	.184	.254	.283
12, 9	.153	.184	.251	.278	25, 15	.153	.185	.258	.289
12, 10	.153	.184	.252	.279	25, 20	.153	.186	.260	.291
12, 11	.153	.184	.253	.280	25, 25	.153	.186	.261	.293
12, 12	.153	.184	.253	.282	30, 5	.150	.179	.240	.263
14, 6	.153	.182	.244	.269	30, 10	.152	.184	.254	.284
14, 8	.153	.184	.250	.276	30, 15	.152	.185	.259	.290
14, 10	.153	.184	.253	.281	30, 30	.153	.186	.262	.294
14, 12	.153	.185	.254	.283	40, 5	.150	.179	.240	.263
14, 14	.153	.185	.255	.285	40, 10	.152	.184	.254	.284
16, 4	.151	.178	.231	.251	40, 15	.152	.185	.259	.290
16, 6	.152	.182	.244	.269	40, 20	.152	.186	.261	.293
16, 8	.153	.183	.250	.277	40, 40	.152	.186	.263	.296
16, 10	.153	.184	.253	.282	50, 5	.150	.178	.239	.263
16, 12	.153	.185	.255	.284	50, 10	.151	.183	.254	.284
16, 14	.153	.185	.256	.286	50, 15	.152	.185	.259	.290
16, 16	.153	.185	.257	.287	50, 20	.152	.185	.261	.293
					50, 25	.152	.186	.262	.295
					50, 50	.152	.186	.264	.298
					∞, ∞	.1517	.1869	.2684	.3035

able. Burr (ref. 19, p. 1094) published a table for all pairs $m, n \geqq 4$, $m + n \leqq 17$, and $P < 0.01$. Later Stephens (ref. 20), extended the table for large values of n and m up to $m = n = 50$.

Watson's $U^2_{n,m}$ test is sensitive for all kinds of deviations between two populations. Table 9 is adapted from reference 20.

$V_{n,m}$ TEST

Another nonparametric two-sample test, Kuiper's modification of a test by Smirnov, is now known as the $V_{n,m}$ test. It is described in detail in reference 1 (p. 35). Maag and Stephens (ref. 29) have provided tables for the critical values of the test statistic. They range from $n = 3$ to $n = 10$ and from $m = 3$ partly up to $m = 20$.

MULTISAMPLE TESTS

In orientation problems, sometimes more than two samples have to be compared with each other. Tests designed to discover differences among several samples are often called tests of homogeneity.

A test for comparing the mean directions of several circular samples was proposed by Watson and Williams (ref. 21). It is assumed that q samples of sizes $n_1, n_2, \ldots, n_q$, respectively, are taken from q circular normal

(or von Mises') distributions with the same unknown parameter κ of concentration.

The null hypothesis states that the mean directions of the q normal distributions are the same. To test the null hypothesis we calculate for each sample the length R_i of the resultant vector using formulas (4) and (5). We also pool the q samples and calculate for all

$$N = n_1 + n_2 + \cdots + n_q \qquad (28)$$

observations the length R of the resultant vector. Then the test statistic is

$$F = \frac{(N - q)(\Sigma R_i - R)}{(q - 1)(N - \Sigma R_i)} \qquad (29)$$

If F exceeds a certain critical value, the null hypothesis of equal mean directions is rejected. The test statistic F is approximately distributed as Fisher's $F_{q-1,\,N-q}$ with $q - 1$ and $N - q$ degrees of freedom. Critical values of F can be found in any table of the F distribution, e.g. in the well-known table by Fisher and Yates (ref. 22) on pages 47, 49, 51, 53, 55. There F is denoted by e^{2z}.

For the rationale of the test and for a biological example see reference 1 (section 22).

A modification of Watson's and Williams' test was recently proposed by Stephens (ref. 23). For the two-sample case, Stephens' test is exact. In the multisample case, the accuracy is improved by the introduction of a factor C that depends on R/N.

These tests are parametric; that is, they are based on strict assumptions on the underlying distributions. They are certainly powerful, but the power may be outweighed by doubts about the basic assumptions. It is therefore desirable to apply nonparametric tests whenever we have no evidence of unimodal distributions with the same degree of concentration. A nonparametric multisample test was proposed by Maag (ref. 24). It is an extension of Watson's U^2 test (see the previous section). Unfortunately the test cannot yet be applied since a table of critical values for the test statistic is not available.

A generalization of the Mardia-Watson-Wheeler test to the multisample case will soon be published. For this test critical values of the test statistic will be available (see refs. 25 and 26).

COSINOR METHOD

In the statistical analysis of biological rhythms a method has been developed that is strongly connected to circular distributions. If the period T of a cyclic phenomenon is known, it is natural to associate the quantity measured with a circle. As the time increases by one period, we rotate once around the circle. As a rule, there will be a time instant when the quantity reaches a maximum. This time instance corresponds to the mean direction of a unimodal circular distribution.

To be more specific, we consider the data in figure 17.[5] The interperitoneal temperature of a rat is measured at various times during the 24 hours of a day, not necessarily at regular time intervals. The data suggest the following model:

$$z_i = C_0 + C \cos(\omega t_i - \varphi) + e_i \qquad (30)$$

where t_i ($i = 1, \ldots, k$) are the time instants at which the measurements z_i were taken. C_0 denotes the mean level of z_i, C the amplitude, $\omega = 2\pi/T$ the known angular frequency, and φ the so-called acrophase, that is, the phase at which the peak of the quantity z

[5] I am indebted to F. Halberg, University of Minnesota, Minneapolis, for the permission to use his data.

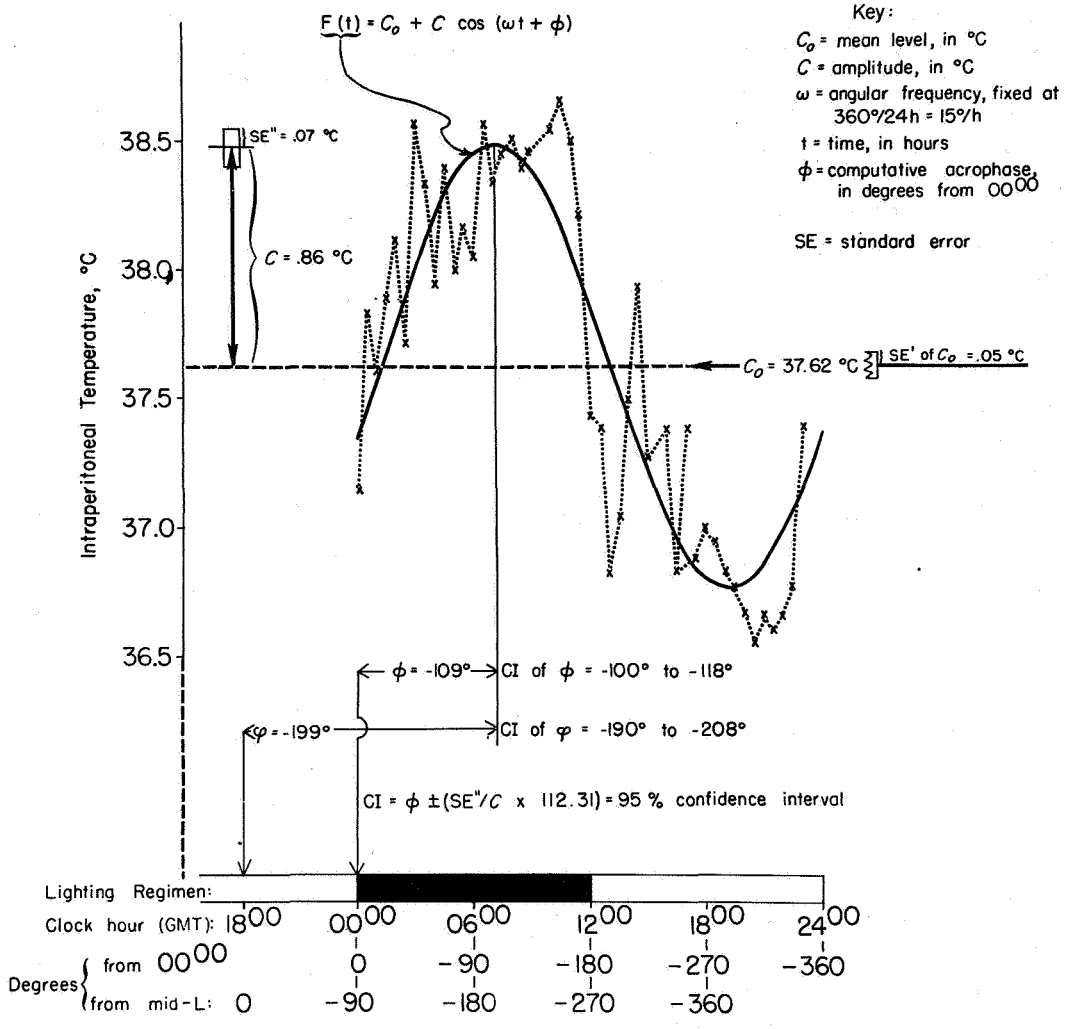

FIGURE 17. Application of the Cosinor method to telemetric measurements of intraperitoneal temperatures of adult female rat. Rat is subjected to special lighting regimen which influences the acrophase. Data were obtained in preparation for a space shot.

occurs theoretically. Finally e_i is the error term.

In order to apply the standard technique of least squares estimation we assume that the errors e_i are independently distributed normal variates with mean zero and common variance σ^2.

The model is not linear in the unknown parameter φ, but it can be linearized by rewriting

$$C \cos(\omega t_i - \varphi) = C \cos \omega t_i \cos \varphi + C \sin \omega t_i \sin \varphi \qquad (31)$$

and by substituting

$$C \cos \varphi = x,\ C \sin \varphi = y \qquad (32)$$

Thus C and φ are replaced by new parameters x and y. Notice that x and y can be interpreted as rectangular components of a vector of length C and polar angle φ.

It is not the place here to present the method of least squares estimation. We mention only that we get minimum variance estimates $\hat{x}$, $\hat{y}$, $\widehat{C_o}$ for the unknown parameters and an estimate s^2 for the unknown variance σ^2 of the error term.

Estimates for C and φ are found by solving the equations (32) with x and y replaced by $\hat{x}$ and $\hat{y}$, respectively.

If measurements are not only taken from one individual but from n comparable individuals independently, we obtain a sample of estimates

$$\widehat{C_{0j}},\ \widehat{C_j},\ \widehat{\varphi_j} \qquad j = 1, \ldots, n \qquad (33)$$

The biological interest usually focuses on the amplitude and the acrophase. It is then natural to plot the n vectors with polar coordinates C_j, φ_j or corresponding rectangular coordinates x_j, y_j in an xy-coordinate system. If our bivariate sample is roughly unimodal, it makes sense to calculate the components of the sample mean vector:

$$\bar{x} = \frac{1}{n} \Sigma \widehat{x_j},\ \bar{y} = \frac{1}{n} \Sigma \widehat{y_j} \qquad (34)$$

This mean vector in turn defines a mean amplitude and a mean acrophase for the sample.

Let μ_x and μ_y denote the rectangular coordinates of the true but unknown mean vector. We may then be interested in a confidence ellipse that covers the point (μ_x, μ_y). For this purpose we follow again a standard technique and determine the sample correlation coefficient r and the standard errors S_x and S_y of $\widehat{x_j}$ and $\widehat{y_j}$. Then the point (μ_x, μ_y) satisfies the inequality

$$\left(\frac{\bar{x} - \mu_x}{S_x}\right)^2 - 2r\left(\frac{\bar{x} - \mu_x}{S_x}\right)\left(\frac{\bar{y} - \mu_y}{S_y}\right) + \left(\frac{\bar{y} - \mu_y}{S_y}\right)^2 \leq (1 - r^2)\frac{2(n-1)}{n-2} \cdot F_{2,\,n-2} \qquad (35)$$

Here $F_{2,\,n-2}$ denotes Fisher's F for a preassigned confidence coefficient. The inequality (35) defines the desired confidence ellipse.

The confidence ellipse informs the research worker to what extent he can rely on the estimated mean amplitude and mean acrophase. If, for instance, the confidence ellipse does not cover the point $(0, 0)$, we conclude statistically that the amplitude is significantly different from zero.

Conversely if the confidence ellipse covers the point $(0, 0)$, then we have no reason to assume that there exists a nonzero amplitude. In this case, periodicity of the quantity z cannot be established.

This method and related techniques, proposed by Halberg and coworkers, have become known as Cosinor method. For a more detailed account see reference 27. It is expected that the Cosinor method will not only be useful in the area of biological rhythms as hitherto but also in some problems of orientation.

There are other statistical methods which also deal with biological rhythms. For a remarkably clear treatment of periodic regression, see reference 28 (chapter 17).

DISCUSSION

WILLIAMS: A number of us have been going to extremes to get not only the point on the circle or

vanishing point but also to develop a statistic that will express the degree of orientation of a track. The problem essentially is this: Given two sets of radiating lines, radiating in some primary direction, other than just plotting where they intersect a circle, how can one determine whether these represent two different populations? Secondly, how can we develop a statistic that will express the straightness of the plot?

BATSCHELET: To express the degree of orientation we may subdivide the track into a moderate number of sections, each of them with the same flying time. We replace each section of the track by a straight line and represent their directions by unit vectors. Then we calculate the mean vector as usual. Its angle serves as mean angle, and its length r is a measure of concentration. We may also use the angular deviation $s = [2(1-r)]^{\frac{1}{2}}$ as a measure of dispersion.

Since each radiating line can be replaced by a straight line with a certain mean angle, a set of radiating lines can be considered as a circular sample. If such a set is a random sample from a population, circular tests can be applied. Likewise for two sets, circular two-sample tests are applicable.

The straightness of a plot can be statistically expressed in many different ways. One such way is using the length of the mean vector as described before. Another statistic or index would be the maximum deviation from a straight line joining initial and end points of a track. Whatever statistic we use, we have to keep in mind that we lose some information and that there will be no definition that serves all purposes.

Special difficulties arise if the animal follows a geographic line or is watching for a food source. Under variable atmospheric conditions the track could also be the result of a learning process.

CARR: What do you think about that series of 10-minute duty-cycle heading reports mentioned by Mr. Baldwin this morning? You suggested that these could not be evaluated statistically because the animal had perhaps learned something between each successive heading. I don't understand this. Why can't each reported heading be considered in the same light as a single sally of an experimental bird in an orientation arena and regular circular statistics applied?

BATSCHELET: A statistic for the "straightness" of a track could be quite suitable to express how well an animal is keeping a certain direction. However, the question may be more demanding: Is the animal heading for a particular destination or can the track be explained otherwise, say by random movements? With one single animal this question cannot be solved by today's statistical methods. We should first create appropriate models for animal migration. Such models would belong to the large area of stochastic processes. Then statistical methods would have to be developed to test whether an observed track fits the model. A random sample of a few animals seems to be the easiest method to solve the problem of how well the animals are motivated.

WATERMAN: We are all very concerned with these problems of experimental design and data analysis for orientation. One great difficulty is that we know almost nothing about the dynamics of orientation, consequently we do not really know what endpoints to use. We can take as many observations *ad lib*, but are they really independent?

Another problem which is prominent in our research on *polarotaxis* is multiple peak orientation. It is difficult to decide how many significant orientation peaks you really have. In addition, we are also interested in knowing the location of these peaks and estimating the significance of their differences.

BATSCHELET: Multiple peak orientation occurs quite frequently. It is essential in each experiment to find out the reasons for this behavior before statistical methods are applied. Once the theoretical peak directions are defined, statistics is able to test the goodness of fit or to decompose a multimodal distribution into unimodal distributions. However, counting peaks without a biological or physical model is a hopeless statistical enterprise.

CARR: Suppose you put out a mechanical turtle with a built-in orientation system and you want to answer the question, Is the machine orienting or travelling at random? Is there no statistical way for evaluating its capacity simply to hold a course? Is there no test for significance for a segment of a course, in terms of its adherence to a straightline or to some regular modification of a straight line?

BATSCHELET: In principle it can be solved, but in the graphs I have seen, it cannot be handled that way.

BALDWIN: What is your opinion of the validity of comparing the paths of two turtles released simultaneously, assuming that there is no communication between them?

BATSCHELET: Whether two turtles released at the same time move independently of each other cannot be tested by statistical methods.

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State of the Art—A Review

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A LOOK AT THE SUBJECT MATTER of this symposium reveals a prime interest in three sets of information relating to the animals under investigation: Where are you? What are you doing? What's it like outside? It is from these data that the investigator hopes to deduce answers to his primary questions relating to How...? or Why...?

Instrumentation developed over the years to help answer some of these questions includes: transducers to sense the data of interest and convert it into something that can be handled and transmitted or stored; transmitters to send the data from one place—usually the animal—to another—usually the investigator; receivers to receive the data and convert it back into some form intelligible to the human senses, or suitable for storage; processors to render the data more suitable for the final step in the process—interpretation.

It would be possible to treat a review of this nature in a variety of ways. I shall restrict my approach here to looking at those methods and devices that are in current use in more than one isolated laboratory, unless something unique is of sufficient merit to warrant broader use.

Transducer classification will be by function rather than by the physical principle employed in the transduction. Two terms will be used that require explanation: passive and active transducers. Passive transducers require an additional source of energy to extract the information about the energy that you wish to measure. Active transducers convert one form of energy directly into another. Examples would be the thermistor which requires application of current to extract the temperature information and thermocouples which are in themselves sources of current related to their temperature.

The overriding considerations in all animal-borne transducers are size, weight, and power consumption. Secondary considerations are related to the ease with which a transducer can be matched to a data transmission link and the details of the circuitry that may be involved related to the accuracy or precision (or both) of the data required.

Time is usually inserted into the data at the recieving end of a given data link. The only real problem with time relates to the need for integration of data for (essentially) instantaneous transmission to a satellite or for storage. It will be impossible to unscramble, say, an integrated record of light level to determine when it was at a maximum.

Sound can provide much information but requires considerable channel bandwidth for

its transmission. Using the same channel it would, for instance, be possible to transmit five or more pieces of information such as temperature, pressure, light level, etc., in the same "space" as one speech channel. Transducers for sound are sensitive to sound pressures from about 0 dB SPL up—(sound pressure level of 2×10^{-4} dynes/cm^2 RMS, which is roughly the threshold of normal binaural human hearing at about 2000 Hz). (See *Audio,* July, Aug., 1969 "A Primer on Sound Level Meters.")

Movement of any sort is accompanied by sounds or accelerations. A rule of thumb for acceleration transducer sensitivity is an output of 1 mv per "g" (982 cm/sec^2) per gram of transducer weight—with a lower limit of that weight being in the order of 2 grams (e.g. a 10-gm transducer would put out about 10 mv/g). It has been amply demonstrated that the observant investigator can quite often correlate other recorded variables with gross animal movements, relating changes in a radio frequency telemetered signal with wing beat, for example.

Position in three dimensions requires one angle and one distance to be measured, as with radar technique, or the less expensive triangulation with three angles from two known baselines. A variation on the latter employs the phase-lock receiver, which can achieve an accuracy of about $\pm$ 1° at 45° or about $\pm$ ¼° at 15°. At 1 km a $\pm$ 1° resolution means location accuracy to about $\pm$ 15 m in two dimensions. Using radar techniques it is quite possible to locate airborne targets to better than 10 times this precision and hence to an accuracy limited only by the accuracy of the original surveying of the instrument site. Radar technique is not the technique of choice for ground targets because of the response from all other matter surrounding the animal. This "ground clutter" will usually obscure any response from a surface animal. Using sonar techniques in water, it is possible to track an uninstrumented 1-kg animal over a range of ½ to 1 km with reasonable assurance that one has been following the same animal. Both of these techniques are treated more fully by other participants of this symposium.

Position over a short range, or within a confined area, may be obtained for an instrumented animal to a precision limited only by the complexity to which the experimenter is willing to go. By dividing the ground area into small areas and interrogating each in sequence, or by criss-crossing the area with "U" or "hairpin" antennas and determining which intersecting area is involved, it is possible to create a time-location diagram.

Direction of motion may be inferred from a series of position data; however, no detail may be read into such data. Actual animal headings, implying, for example, the compensation for cross-wind or current, must come from instrumentation carried by or intimately related to the animal. Such instrumentation is not yet available in light, compact form.

Cost of maintaining watch over a particular animal for a significant period of time during a migratory or other protracted voyage is high. As other members of this gathering will relate, aircraft of all kinds—fixed and rotary wing, free and powered balloons—have been employed at various times with varying success. It is not germane to enter here into the discussion of the influence of a following aircraft on the normal patterns of behavior of a bird, or of a following boat on the normal pattern of an aquatic animal, or of a following field vehicle or safari on the pattern of behavior of a land animal. Nor is it germane to do more than bring up the obvious that equipment mounted on (or in) any animal will affect its behavior in some way, and that we can probably relate fairly

directly the effects on behavior of any abnormality perceptible to the animal. The corollary to this is that an instrumentation system must strive to have its animal-borne component be as insignificant to the animal as the ingenuity of the investigator can achieve—or pay for.

Environmental conditions that may influence behavior, or which may be used as clues to explain behavior include light, sound, temperature, pressure, and magnetic fields.

Light levels in the environment can be measured to a lower limit of the (usually) electrical "noise" in the instrumentation system, or the "dark current." This will tend to limit the usefulness of such transducers as the passive photoconductive diode to 10 ergs/cm^2 sec in an uncomplicated system suitable for animal-borne equipment. Of the various photodetectors available, the photoemissive tube would be of choice because of speed or response and stability if it were not for its large size, fragility of the evacuated or gas-filled glass envelope and the requirement for a relatively high voltage on its anode (45 to 200 V). Photovoltaic cells (active cells) may be totally adequate if the light level range is restricted to about 100:1 and the temperature range is less than $\pm 10°$C—or is independently measured for correcting purposes. The main disadvantage to the resistive photodiode is its relatively sluggish response to falling light levels and its "light memory," which restrict its usefulness to absolute measurements over a range of about 1000:1 in a temperature range of $\pm 10°$C.

Polarized light requires the addition of a filtering device and the ability to orient the device in known directions, or to know several specific orientations—to divide the universe into a few steps or many, depending upon the needs of the experiment.

Temperature transducers in this context have been empirically narrowed to the use of passive thermistors—devices that change their electrical resistance with temperature. They are small, light, and with reasonable care are more accurate than any other method. The precision available is also in excess of any but the most sophisticated (and hence complex) of other methods. Thermistors have the added advantage of often being usable as a circuit component in a conventional radio transmitter, with considerable saving in complexity and power use. Typical sensitivity achievable will be in the range of 3- to 5-percent resistance change per degree Celsius. Physical size ranges from a minimum of "pinhead" to 1 or more cubic centimeters.

Pressure of the atmosphere can be transduced as well as the transducer can be sealed. The transducer usually employs a diaphragm and a sealed chamber, with means for passively determining the diaphragm deflection using strain gages or by electrical inductance or capacitance changes. Since these latter can often be employed with minimum additional circuitry to directly affect a radio transmitter, they are often the method of choice. Typical sensitivity achievable with simple systems is 2 to 10 mm Hg. Pressure measurements within an animal employ similar techniques but include some means for equalizing the long-term ambient pressure changes to give only the short-term changes. Sensitivity will be in the same range, limited again by sealing techniques.

Magnetic fields remain somewhat of an enigma. Direction can be sensed by time-honored methods, but magnitude cannot. Transducers with outputs in the range of microvolts per gauss are not useful here but are representative of the state of the art.

Transmitters of position or other data that are attached to animals in the context of migratory or other long voyages that would appear to require orientation and navigation are usually radio. Over short distances light

or sound sources, and over very short distances, atomic radiation sources have been used, and some of these are reported by others that follow in this symposium. In the main, however, the radio transmitter is the method of choice, and the theoretical limitations are well known and understood. Typical "thinking numbers" would include a minimum transmitter of about 10 grams to achieve an air to ground range of 5 km or a ground-to-ground range of ¼ km, with a useful life of 1 month. Additional life may be had at the expense of weight at the rate of about 10 grams per additional month required. Generalizations of this nature are very dangerous, since there are so many variables that enter into the solution to a given specific problem. By rigid optimal design 2 grams can be made to achieve what 20 grams might achieve under other circumstances in which some other boundary condition was limiting.

A review of progress over the last 8 to 10 years—since the last organized gathering of this nature—reveals that there are many more people who are using particularly radio telemetry techniques today to assist them in getting data from and about navigation and orientation functions in animals. The equipment itself is still very similar to that described at the meeting of March 1962 at the American Museum. Individual electronic parts have decreased in size to the point where the power supply and antenna size tend to be limiting. There is also still a dearth of commercial sources for completed equipment, so that much progress is slowed because of dependence upon empirical development by the wrong people. Signal processing, when needed, is under about the same constraints as the transmitter, in that, when the expense can be justified, integrated circuitry can achieve volume compression to about 0.25 cc per channel. There has not been any breakthrough development in transducers suitable for uses in this field, so that electrodes still cease to be effective after 3 to 6 months, pressure still requires about 0.2 cc for a transducer with about a 3-month life, and there is no immediate prospect of using subminiature ion sensing electrodes for studies of more than a few days duration.

One advance that has taken place is the development of a more successful sealing compound—a mixture of 100 parts paraffin wax (Atlantic Refining # 131) and 20 parts Elvax 260 (DuPont Co.). This has been shown to retain resistance to body moisture penetration over a 37 000-hour period in excess of 10^{13} ohms across about a 0.125-mm film. Its use under a surface protecting film of silicone rubber is recommended. Since the silicone rubber is permeable, a finished assembly may be chemically sterilized.

It would be very pleasant indeed if I could report more spectacular progress. Perhaps the discussion period will bring some out.

For those of you involved in the daily use of these techniques, I would recommend two books of recent vintage: Mackay's *Bio-Medical Telemetry: Sensing and Transmitting Biological Information from Animals and Man* (2nd Ed., Wiley, 1970) and Geddes and Baker's *Principles of Applied Biomedical Instrumentation.* (Wiley, 1968) There are others to which these two will lead you.

SESSION II

Animal Tracking

Chairman, ROBERT GALAMBOS

Satellite and Ground Radiotracking of Elk

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RADIOTRACKING AND MONITORING of free-living animals in natural environments is providing an effective new technique for acquiring information on biological processes, including animal orientation and navigation. To test the practicability of extending the technique by using satellite systems for tracking animals, a female elk was instrumented with an electronic collar. It contained both the Interrogation Recording Location System (IRLS) transponder and a Craighead-Varney ground-tracking transmitter. The elk was successfully tracked and monitored by satellite during the month of April 1970. This was the first time an animal had been tracked by satellite on the surface of the Earth. Information derived from the present feasibility study provides a basis for assessing uses of the system, reducing the weight, and improving the configuration of the instrument collar for monitoring a variety of large mammals. The minimum weight of the IRLS transponder, even with microminiaturization, makes its use impractical for most small mammals and birds. A doppler-shift type of satellite system, as described by Maxwell at this conference, may prove effective for small animals.

This project was a joint endeavor between the Smithsonian Institution and the National Aeronautics and Space Administration, conducted in collaboration with the Montana Cooperative Wildlife Research Unit, the Environmental Research Institute, the State University of New York at Albany, and the National Geographic Society. Pretesting was conducted at the National Bison Range, Moiese, Montana. The experiment was carried out at the National Elk Refuge, Jackson Hole, Wyoming, in cooperation with the U.S. Bureau of Sports Fisheries and Wildlife, the Wyoming Game and Fish Commission, the U.S. Forest Service, and the National Park Service. Previous research under NSF (G-17502) made possible the use of the ground radiotracking system.

HISTORY OF PROJECT

The present project had its inception on May 26, 1966, at a conference sponsored jointly by the Smithsonian Institution, the

American Institute of Biological Sciences, and the National Aeronautics and Space Administration (ref. 1). At this time the possibilities for using the Nimbus meteorological satellites for tracking and monitoring wild animals were explored by biologists and engineers. An initial estimate of 11.3 kg for the IRLS instrument platform proved accurate. This transponder was heavy for use on wild animals, as it had been designed for oceanographic buoys and high-altitude weather balloons. It was apparent that a large animal would be required for the first experiments in satellite tracking of free-roaming animals. However, engineers calculated that the weight could eventually be reduced by 50 to 75 percent. An elk was chosen for the first test because of its large size (about 225 kg), gentleness, and migratory behavior. In addition an accumulated background of experience in radiotracking and immobilizing elk (ref. 2) was available over a period of years in the Jackson Hole–Yellowstone National Park area. Logistic support for the project was particularly favorable in the Jackson Hole area.

A planning conference was held May 9–12, 1969, in Missoula, Montana, at which time biologists and engineers decided on the configuration and packaging of the IRLS transponder and selected parameters to be monitored. A Craighead-Varney transmitter was packaged with the IRLS transponder since this ground-tracking system had a capability that enabled observers to visually locate the elk, thus providing direct observations with which to measure the accuracy of satellite positioning. This 32.0 MHz tracking system had been used to successfully track six cow elk for a total of 1216 animal tracking days. In addition, one elk had been radiotracked from the National Elk Refuge to its summer range in Yellowstone National Park, a distance of 64.4 airline km.

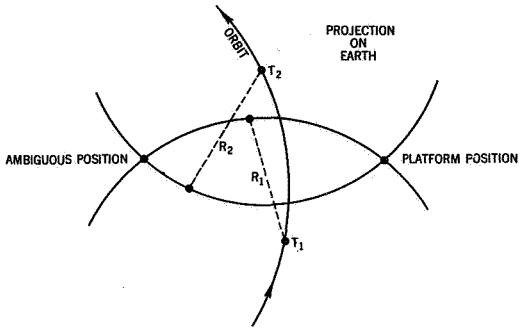

FIGURE 1. IRLS location technique: Distance (R_1) between satellite and instrument platform generates a sphere with satellite at center (T_1): this sphere in space intersects the Earth in a perfect circle. Second perfect circle intersecting first at two points is formed by second interrogation at T_2. Platform position is readily selected on basis of prior information from previous orbits.

MATERIALS AND METHODS

The experiment was carried out with the Nimbus III and IV satellites, using the IRLS system to locate and interrogate the animals (refs. 3 to 5). The IRLS instrument was designed with 28 channels of communication, 10 of which were used in the present experiment. One IRLS instrument was modified and packaged into the collar for the elk, with batteries as the source of power and solar cells to maintain battery charge. To conserve power, a timing system provided a 10-min window for transmission during satellite overpasses. The radio transmitter power output was 15 W to the antenna at a frequency of 466.0 MHz.

The Nimbus satellites are in polar-sun-synchronous orbits, and their exact position above the Earth can be calculated. The distance between the satellite and elk was determined by a radar-like interrogation. This line generates a sphere, with the satellite at the center, that forms a perfect circle where it intersects the Earth's surface. An-

other circle is formed by the second interrogation, intersecting the first circle at two points. The animal is located at one of these two points; the other point is sufficiently distant from the animal, as determined by prior information, to be considered unlikely as the animal's position (fig. 1).

The Craighead-Varney ground-tracking transmitter (32 MHz) was installed in the lower compartment of the collar. Batteries and antenna for this system were located at the top of the collar.

The instrument collar was separable into two parts for installation on the elk. Instrumenting was accomplished when the animal was immobilized with M99 (etorphine). Ten min were required to make the electronic connections and fasten the collar on the elk.

Internal telemetry for the instrument was provided by five sensors, and external data were monitored by another five sensors. The data format corresponding to the computer printout is shown in figure 2. One such frame of data was collected during each interrogation of the instrument. For each overpass the satellite was programmed for up to five interrogations at intervals of 1.5 min. Data were available to the experimenters within 1 to 2 hr of the overpass. The pressure transducer for measuring altitude failed and was inoperative throughout the experiment. Skin temperature was measured by a thermistor mounted on a tension arm attached on the inside surface of the collar. Battery voltages and temperatures were monitored directly, and the received signal strength was obtained at the output of the first intermediate frequency stage. Two thermistors provided overlapping scales (—40 to + 10 °C; 0 to + 50 °C) for measuring ambient temperature within ± 1 percent accuracy. For additional information about the IRLS system see Craighead et al.

An electromechanical timer-control unit

DATE OF RUN MO. DAY YR.
4 28 70
ORBIT NUMBER 5082
PLATFORM ID 105452 ELK

COMMAND TIME HH MM SS.S
07 54 10.6
FRAME 1

DATA RECEIVED

2 UNUSED	1 UNUSED
4 ALTIMETER	3 UNUSED
6 +12 VOLT BATTERY	5 RECEIVER SIGNAL
8 BATTERY TEMPERATURE	7 SKIN TEMPERATURE
10 -40 TO +10°C AMBIENT	9 0 TO +50°C AMBIENT
12 TIMER	11 +4.8 VOLT BATTERY
13 to 28 UNUSED	13 LIGHT INTENSITY
	14 to 27 UNUSED

COMPUTED PLATFORM LOCATION

LAT.	LONG.	TIME DAY	HH	MM	SS.S
43.492N	110.721W	118	07	54	11.0

FIGURE 2. Data format showing arrangement of data on computer printout forms.

provided a 6-month battery lifetime by completely unloading the battery during the 12-hr intervals between orbital overpasses. During each overpass a 10-min "power on" period was initiated precisely as the satellite came into radio view. The timer setting of the window was monitored on each orbit, and periodic adjustments were made by command from the satellite to maintain synchrony.

PROCEDURE

During the summer and fall of 1969 a mockup model of the instrument collar was developed and tested on four female elk in a corral at the National Bison Range. The collar (11.3 kg) weighed less than known weights of elk antlers. None of the elk experienced any apparent interference with daily activities, and there was no evidence of breakage of hair or skin abrasions from rubbing of the collar during feeding activities. One elk carried the collar for a period of 90 days without difficulty. Pretesting of the electronic instrument collar began on January

20, 1970, using the same female elk after it had been without the mockup collar for about 2 weeks. The pretest was highly successful in terms of placing the instrument collar on the elk and interrogating the instrument daily for the next 12 days on 16 orbits of the satellite.

On February 5, two female elk at the National Elk Refuge were immobilized and fitted with mockup collars to pretest the reaction of these animals to the collar prior to instrumentation.

On February 19, an effort was made to place the IRLS collar on one of the two females wearing the mockup collars. The elk were uneasy as a result of a census of the herd made earlier that morning, and the experimental animal was difficult to approach. Considerable maneuvering was required to get one of the females within range of the immobilizing gun. The shot made at long range (60 to 70 m) missed the intended elk and struck another female in the herd. She became immobile in about 5 min. This female appeared to be a healthy individual, and except for preconditioning to the collar, equally well suited for the experiment as either of the females wearing mockup collars. Since conditioning did not appear to be essential, the instrument collar was fastened to this elk with the assistance of electronic engineers. The female recovered quickly upon receiving the antidote M285 (diprenorphine) after being immobile for 30 min. The female then rose to its feet without difficulty, stood momentarily looking at the haywagons and observers without apparent alarm, and then ran to rejoin the herd. The satellite was unable to communicate with the instrument collar for the first 3 days, apparently because installation of the instrument package had occurred during the hourly 6-min speed-up cycle, which in turn disrupted the orbital period setting of the timer. By special command from the satellite the timer was reset, and at noon on February 22, data were received from the animal. Subsequent passes failed to yield data. Visual observations of the elk indicated that she remained bedded down for abnormally long periods of time, walked sluggishly, and was not feeding. The female finally died on the morning of February 23, apparently of pneumonia which is not uncommon in the herd on the Refuge. The stress of being captured may have aggravated an incipient infection.

On April 1, 1970, one of the two females originally fitted with a mockup collar was instrumented with the IRLS equipment (fig. 3). A veterinarian ascertained the health of the animal. Her body temperature was normal (38.5 °C) and she appeared to be in good condition. She became immobile 5 min after administration of the M99 drug and remained immobile for about 27 min, during which time the dummy collar was removed and the electronic collar was attached. Immediately after the antidote was injected the

FIGURE 3. IRLS instrument collar on female elk tracked in April 1970. Antenna housing is at top and solar panels are on side of collar.

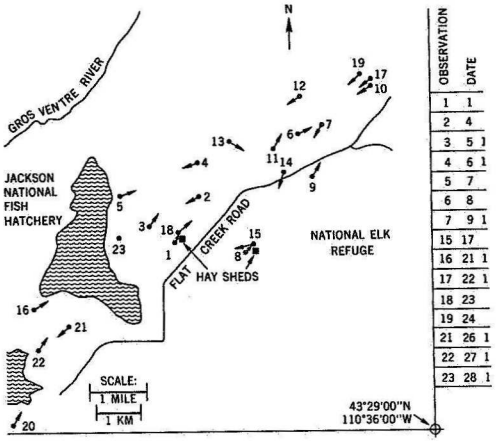

FIGURE 4. Locations of instrumented elk from direct observation or fixes with Craighead-Varney ground-tracking system. Accuracies were within 0.5 km. Errors in satellite fixes were computed against these observations. Arrows indicate direction of following observation.

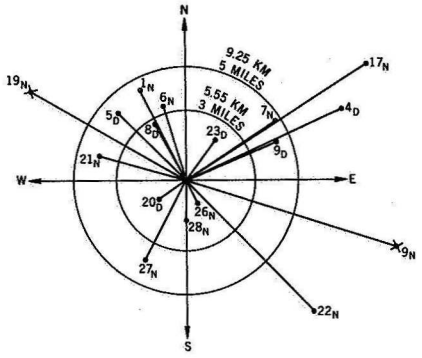

FIGURE 5. Visual observations vs satellite positions.

female was placed on her brisket. Within 3 minutes she arose, looked around briefly at the observers and then nibbled at a nearby bale of hay. The instrumented female then walked off about 25 m, stopped, and then slowly ran off to join the herd about 200 m away. When she joined the herd she immediately had an encoutner with another female. Both elk rose on their hind legs and paddled gently with their forelegs. Such behavior seems to establish dominance-subdominance relationships between individuals within the herd. This incident and the immediate acceptance of the instrumented elk by other members of the herd indicated that the process of immobilizing and instrumenting had not been traumatic and that the female returned to normal behavior almost immediately after recovering from the drug. Within the next hour the instrumented female was observed feeding, standing, and walking with the herd.

The elk had recovered and joined the herd by 10:50 a.m. At approximately 11:00 a.m., Nimbus III passed over the Jackson Hole area and the IRLS collar transmitted location, skin and air temperatures, and five parameters of the IRLS instrument (table 1).

RESULTS

The resolution of locations determined by the satellite varied considerably. In order to measure the accuracy of the locations it was necessary to derive a set of reference points from field observations of the elk. Orbital overpasses were approximately at noon, and some of the observation times did not coincide exactly with satellite overpasses, making some interpolation necessary in deriving the set of reference points. The reference points made on the ground are shown in figure 4. The magnitude and direction of location errors determined by satellite are shown in figure 5. Three locations were beyond the scale and were not included in the figure. Excluding these three points the mean errors were 4.8 km in latitude and 6.2 km in longitude. The large east-west errors (longitude), which were typically less than the north-south errors (latitude), reflected the fact that

TABLE 1.—*Locations and Sensory Data from Elk at National Elk Refuge*

Orbit no.	Date	Time (GMT)	Location		No. frames	Channel Numbers								
						5	6	7	8	9	10	11	12	13
			lat.	long.		Signal strength volts	+12 volt battery °C	Skin temperature °C	Battery temperature °C	0°C to +50°C ambient temperature	−40°C to +10°C ambient temperature	+4.8 volt battery	Timer (min)	Light intensity [a]
Nimbus III														
23	Apr. 1	07:49:13	43.62	110.74	4	1.15	12.45	<15.5	+5.0	<0.0	−5.5	5.1	5 to 6	6.35
27	Apr. 1	18:07:08	43.51	111.14	3	1.00	12.8	<15.5	+5.0	<0.0	−1.5	5.25	6 to 7	2.45
40	Apr. 2	07:05:14			1	.25	12.95	24.0	+.5	<0.0	−4.5	5.35	5 to 6	6.35
53	Apr. 3	08:07:55			1	.20	13.55	<15.5	+7.0	+1.0	0.0	5.55	4 to 5	2.35
67	Apr. 4	17:43:45	43.588	110.69	3	.10	13.4	19.5	+5.0	+1.0	+.5	5.5	5 to 6	2.55
80	Apr. 5	18:47:44	43.617	110.78	3	.85	13.4	20.3	+12.5	+10.0	+8.5	5.5	4 to 5	2.40
91	Apr. 6	07:47	43.607	110.73	4									
03	Apr. 7	02:04:09	43.594	110.598	4	.30	13.25	20.5	+4.5	+1.0	+.5	5.35	5 to 6	6.35
18	Apr. 8	08:05:29.2			1	.15	13.3	<15.5	−2.0	<0.0	−7.5	5.35	3 to 4	6.35
21	Apr. 8	18:24:08	43.602	110.678	5	.95	13.65	24.0	+9.0	+2.0	+1.5	5.55	4 to 5	2.65
30	Apr. 9	07:23:44	43.501	110.402	5	.85	13.55	23.5	+1.5	<0.0	−6.0	5.5	5 to 6	6.35
34	Apr. 9	17:40:29	43.589	110.543	4	1.00	13.65	27.8	+8.5	+2.5	+2.0	5.55	4 to 5	2.75
Nimbus IV														
	Apr. 10	18:46:00			2			34.5	+8.0	+5.0	+4.0	5.4	3 to 4	2.95
	Apr. 10	07:44:30			1			37.5	+3.0	<0.0	−1.5	5.2	5 to 6	6.35
	Apr. 17	18:01:00			1			27.8	+4.5	+4.5	+4.0	5.4	4 to 5	3.3
Nimbus III														
4913	Apr. 15	18:39:40.1			1		13.75	27.5	11.0	2.0	1.5	5.60	4 to 5	2.10
4937	Apr. 17	06:58:5.4	43.621	110.485	4		13.30	27.6	3.0	<0.0	−4.0	5.40	7 to 8	6.35
4950	Apr. 18	07:59:16.5			1		13.15	20.0	3.0	<0.0	−2.0	5.35	4 to 5	6.35
4964	Apr. 19	07:17:47.3	43.604	110.852	3		13.15	25.0	1.5	<0.0	−4.0	5.35	6 to 7	6.35
4981	Apr. 20	18:37:43.3	43.517	110.696	3		13.75	26.5	6.5	1.0	0.5	5.60	4 to 5	2.45
4988	Apr. 21	07:37:3.9	43.545	110.794	3		13.55	25.0	−2.5	<0.0	−8.0	5.35	4 to 5	6.35
4995	Apr. 21	17:55:8.6	43.52	110.32	3		13.55	22.0	12.5	1.5	0.5	5.40	5 to 6	3.00

Orbit no.	Date	Time (GMT)	Location		No. frames	Channel Numbers								
						5	6	7	8	9	10	11	12	13
			lat.	long.		Signal strength volts	+12 volt battery °C	Skin temperature °C	Battery temperature °C	0°C to +50°C ambient temperature	−40°C to +10°C ambient temperature	+4.8 volt battery	Timer (min)	Light intensity [a]
5001	Apr. 22	06:55:12.5	43.480	110.553	2		13.25	25.5	−1.0	<0.0	−6.5	5.25	6 to 7	6.35
5015	Apr. 23	07:58:4.9			3		13.25	22.0	1.0	<0.0	−4.5	5.30	5 to 6	6.35
5022	Apr. 23	18:16:28.4	43.568	110.652	4		13.65	30.3	13.5	6.5	6.5	5.40	5 to 6	2.50
5029	Apr. 24	07:12:33.0	43.579	110.267	5		13.15	24.5	2.5	<0.0	−3.0	5.20	3 to 4	6.35
5055	Apr. 26	07:34:17.3	43.492	110.712	3		13.25	<15.5	4.5	1.5	1.5	5.10	3 to 4	6.35
5069	Apr. 27	06:53:19.7	43.452	110.783	3		13.25	28.5	2.0	<0.0	−3.0	5.30	5 to 6	6.35
5075	Apr. 27	18:56:7.0			1		13.55	27.8	8.5	3.0	3.5	5.45	1 to 2	2.55
5082	Apr. 28	07:54:10.6	43.492	110.721	4		13.40	32.2	2.0	<0.0	−2.0	5.30	2 to 3	6.35

[a] 6.35 = night; 2.10 to 3.00 = varying degrees of sunlight

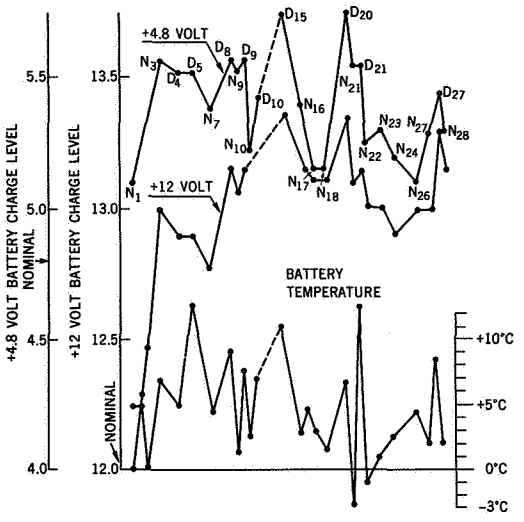

FIGURE 6. Satellite monitored day-night battery voltages and temperatures.

satellite locations are most accurate when the satellite is between 10 and 50° above horizontal. The dipole antenna used in the elk experiment was designed for a coverage above 45° with respect to the horizontal. In future experiments the accuracy of locations can be improved with a low profile, omnidirectional, circularly polarized antenna.

The monitoring of sensors showed the potentialities of the IRLS system for obtaining physiological and environmental information (table 1). The voltage levels of the batteries increased during the first 3 days, showing that the solar panels were responsible for charging the batteries. The charge levels remained near maximum throughout the experiment. The trends in battery and ambient temperatures were identical (fig. 6). Some warming was probably provided by the elk's body. In previous studies of the effects of ambient air temperature on radio collars the battery pack and transmitter have shown an average 9.4° C increase over air temperatures under cold weather conditions. This was attributed to the warming effect of the animal's body (refs. 6 and 7).

The accuracy of measuring skin temperature with a thermistor at the point of contact between the collar and the animal's body requires further testing to determine the effects of the collar in compacting the hair and insulating the thermistor, as well as the effect of movement of the collar during feeding activity. Individual skin readings taken at 1.5-min intervals during interrogation sequences suggest that the animal was at rest when the readings were constant and active when the readings were variable (table 2). Apparently movement of the collar altered its insulating effect, producing more regular temperature readings when the elk was at rest. The exceptionally high skin temperature (37.5° C), which was near body temperature, on April 10 could have resulted from continued pressure of the elk's neck against the thermistor as the animal lay on its side with its neck resting on the collar. In a similar manner a skin temperature of 35.9° C was recorded from an awakened and alert black bear in its winter den as it lay on a thermistor located

TABLE 2.—*Multiple Interrogation Skin Data*

	Elk at rest (°C)		Elk moving (°C)
April 9, night...	23.6	April 7, night.	18.6
	23.6		20.5
	23.3		20.3
	23.0		19.7
	23.0	April 9, day...	27.8
April 17, night..	28.0		27.2
	28.3		28.1
	28.3		23.0
	28.3	April 23, day..	30.9
April 21, night..	25.0		30.0
	25.5		30.3
	25.5		29.9

between the animal's body and the insulating material of its bed (ref. 2). An inverse relationship between skin and ambient temperatures, shown in about half the recordings (fig. 7), could reflect a decrease in insulation of the elk's integument due to compaction of the hair under the collar. The significance of the data is that they show the potentialities for studying thermoregulation by monitoring surface and subcutaneous skin temperature, along with deep body temperature, using the IRLS system.

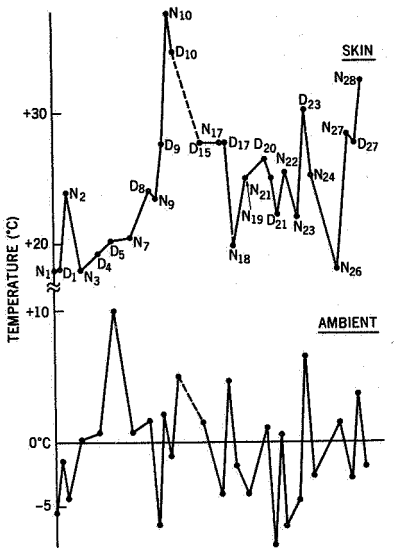

FIGURE 7. Satellite monitored skin and ambient temperature readings.

MOVEMENTS OF THE ELK

Except for the longer movements, the locations obtained with the IRLS system were too inaccurate for determining the local pattern of movement of the elk within the Refuge. However, satellite location of the elk could have yielded useful new information on migratory movements despite the low resolution. The collar rotated around the elk's neck on May 1 and, in the inverted position, contact between the elk and the satellite was lost. Communication proved impossible with the antenna pointing groundward. Until June 10, the elk was located by the ground-tracking system. When the elk moved far or rapidly it was relocated by air, using a Cessna 150 with a small loop antenna attached to the wing strut. Under favorable conditions the signal was received in the airplane from a distance of up to 40 km at altitudes above ground level of 300 to 1000 m; the strength of the signals improved with altitude.

On May 15, the elk moved to the northern portion of the Refuge and was approached, using the directional receiver. She was observed to feed and run well with a band of 15 elk, and she appeared in better physical condition than most of the other elk. Two days later she left the Refuge, moved north along the east side of Blacktail Butte, and arrived the following day in the area of Signal Mountain, 28 airline km from her last position in the Refuge. After remaining here and in this general area for 5 days the elk began moving up Spread Creek on May 25, traveling southward into the Gros Ventre drainage (fig. 8) to Slate Creek where a group of about 300 elk annually calve and range for the summer months (ref. 8). The circuitous route taken by the elk to reach its summer range, covering about 65 km, rather than traveling directly up the Gros Ventre River valley for a distance of about 20 km, was unanticipated. The route taken also involved crossing a high divide that was still snowbound.

As the instrumented elk migrated, the number of elk with which she was associated gradually diminished with distance and time away from the National Elk Refuge. On the Refuge she was a member of a scattered herd of 3000 to 4000 animals, and this number diminished to an average of 250 to 400 animals.

FIGURE 8. Gros Ventre River drainage to which elk migrated from Refuge. Loop antenna, shown at top of the photograph, was used to communicate with ground-tracking system.

On May 15, two days before leaving the Refuge, the elk traveled with a group of 15 animals. On May 23, and from time to time thereafter, she was observed alone or with only one other cow. From this latter behavior we suspected the imminence of parturition.

From May 30 to June 10, sightings and radio fixes indicated that she moved only an average of 1.1 airline km per day with a range of 0.2 to 1.9 km. This was a considerable reduction over her previous daily travel, and might have been related to calving. A close observation on June 8 established that the elk was in good condition, that most of the winter coat remained, and that no abrasions or sores caused by the collar were evident. It also appeared that the cow was not pregnant. A calf was not observed at this time, but could have been hiding, since it is a common practice of calves to hide when danger is imminent (ref. 9). Possibly the decrease in daily movement as indicated by radiotracking was a clue to time of calving. Such noticeable changes in daily movement as revealed by radiotracking, when properly interpreted and then verified by observation, can provide insights to animal activity and behavior. For example, intermittent signals from instrumented grizzly bears have been visually confirmed as an indication of den digging (ref. 10).

An interesting result of the elk's summer movements is that she was more or less constantly traveling, spending only a few days to a few weeks in any one area or drainage. The elk was last located by the ground-tracking radio on June 10. The next contact was a sighting on July 28 in the Cottonwood drainage about 20 km east of Slate Creek. The probable route of her travels (a gradual movement) after leaving the Slate Creek–Mount Leidy area was eastward to the confluence of Poison Creek with Cottonwood Creek. On November 14, she was accidentally shot by a hunter 8 km from this location and just prior to her expected safe return to the National Elk Refuge.

Daily movement of the elk on the Refuge that occurred before migration averaged 3.7 km, based on 41 movements, and ranged from 0.6 to 14.6 airline km. Just prior to a long trek on April 24, ground-tracking showed that the elk had traveled an average of about 2.6 airline km per day. On April 25, she backtracked 14.6 km toward the Refuge feeding lots (fig. 4). This was the longest single trek prior to migratory movement. Such movement back and forth in response to weather and snow cover is typical during April. However, this return travel started before a storm arrived and may have been in response to an approaching storm. The ba-

rometer dropped, and snow fell for the next two days.

Some animals apparently can sense an approaching storm. A change in activity associated with an approaching snow storm was clearly demonstrated while radiotracking an instrumented grizzly bear to its winter den. This grizzly altered her previously recorded daily activity pattern one morning and started moving rapidly toward her den in bright, sunny weather. Snow started to fall in late afternoon, and the female grizzly arrived at her pre-excavated den that evening (ref. 10). Apparent early detection of weather changes by both bear and elk is intriguing and may be related to the animals' possible ability to detect infrasound waves created by approaching but distant storms (ref. 11). Satellite as well as ground radiotracking should be a useful tool in probing this phenomenon in wild animals, perhaps even under controlled conditions.

Changes in the elk's activity and their interpretation, as well as the migratory observations, indicate that behavior and migration of individual elk can be studied in detail with the aid of radiotracking and biotelemetry ground-satellite systems. These studies can provide information of value in the management of elk populations, as well as contribute toward a better understanding of the phenomena of animal behavior and migration.

RESULTS

The study was successful in demonstrating the practicability of tracking large free-roaming animals in natural environments by satellite systems. The prototype IRLS instrument collar was somewhat bulkier and heavier than required, and on the basis of information derived from monitoring the instrument by satellite, particularly the effect of the solar cells on battery charge, calculations indicated a possible weight reduction of about 50 percent down to about 5 kg. A fin antenna is now available for the instrument, which would eliminate the large housing required for the dipole antenna and reduce the profile of the instrument. Variable padding with foam rubber to adapt the instrument to a given elk would solve the problem of the collar turning around on the elk's neck. An improvement in the resolution of locations to within 1 km would be possible with the development of a low profile, omnidirectional, circularly polarized antenna. Experimentation with effective sensory systems is needed to measure deep body temperature, skin temperature, heart rate, and other physiological parameters. To eliminate external wiring, implantable transmitters are required for transmission of data to receivers in the instrument collar. Miniaturized equipment for periodic data sampling and storage prior to transmission (every 12 hr) is needed.

The advantages of satellite systems are described elsewhere (ref. 12). Briefly, satellites permit daily tracking and monitoring on a worldwide scale with instruments that are immune to the effects of Earth's weather and provide data under day or night conditions. Where animals are isolated in polar regions, the oceans, or deserts, satellites are especially useful. To obtain adequate data on bird migrations over long distances and at high altitudes or marine animals covering great distances, satellite systems are almost indispensable. The uniqueness in satellite systems lies in the ability to combine continuous tracking up to 6 months, or longer, with simultaneous monitoring of physiological and environmental parameters.

Despite the advantages of satellites, radio contact with animals from the ground is also needed for homing in on animals for direct observations. An integration of the two systems is likely to be required in most research.

An accurate system for tracking free-living animals and monitoring both physiological and environmental parameters will provide a valuable new tool for investigating the behavior and ecology of wild animals. Satellite systems can aid in investigating a vast array of important biological problems, including migratory movements and navigational guidance mechanisms of animals, patterns of dispersal and concentration associated with feeding and reproduction, the entrainment of physiological cycles by environmental parameters, and patterns of vector trans.nission of disease by migratory animals (ref. 12). The knowledge gained through such studies will help provide the scientific basis for intelligent management of the Earth's ecosystems.

ACKNOWLEDGMENT

We wish to thank biologists Harry V. Reynolds III and Vincent Yannone, and graduate student Steven M. Gilbert of the University of Montana, for their assistance in this project. Joel R. Varney, Research Associate, Montana Cooperative Wildlife Research Unit, University of Montana, contributed significantly to this project in testing and applying the electronic systems. James C. Maxwell, Staff Engineer, Ecology Program, Office of Environmental Sciences, Smithsonian Institution, aided in the pretesting of the IRLS collar.

The IRLS instrument was conformed into the collar for the elk by Radiation, Inc., Melbourne, Florida.

Tracking animals by satellite was stimulated by Sidney R. Galler, Assistant Secretary (Science), Smithsonian Institution, who organized the 1966 conference on this subject. We are grateful for his encouragement and inspiration. George J. Jacobs, Chief, Physical Biology, National Aeronautics and Space Administration, was particularly helpful in the development and administration of the project.

This project was supported by a NASA contract (NASW–1983) to the Smithsonian Institution.

DISCUSSION

COCHRAN: You have called this a feasibility study. Is it practical to conduct a study on the elk?

BUECHNER: Yes indeed, I think it is practical. We know the weight can be reduced at least one half, without doing any miniaturization. We also know how to make a better configuration for the collar and we have some ideas on how to improve the antenna system. The costs can come down. In fact, potentially, if there are enough users, the costs could come down very quickly to something around $2000 or $3000 per instrument package.

We hope that next year we will be able to track an elk during the spring migration and make periodic ground observations to correlate behavior with migration movements and physiological parameters.

ENRIGHT: There may be a slight difference in the elevation of the animal which could make a big difference in the apparent geographical location. Is this a real problem?

COTE: The elevation is certainly a factor; we do not assume that the Earth is a perfect sphere. In the case of the elk, changes were in the order of 90m (300 ft) which did not greatly impact location accuracy. For high flying balloons or aircraft tracking applications the altitude becomes a critical factor and must be entered into mathematical equations for location computation.

WILLIAMS: You state that your readings extended over eight to ten minutes for one point. How is this possible?

COTE: Since the satellite is in view for 4 to 5 min, multiple interrogations lasting 2 sec each are programmed. This allows up to five data samples under normal operational conditions where 1 minute intervals are maintained. The two frequencies utilized in the IRLS system are 401.5 and 466.0 MHz.

CARR: Did resolutions in your track-plots for the elk correspond to those for the buoy? That is, do you get about the same fineness in separating and locating points with the elk as you would in tracking the buoy?

COTE: No. The buoy positions were more accurate since higher power equipment was used. Under these conditions the satellite need not be directly overhead to obtain solid communication. Optimum location accuracies with the higher power equipment are obtained at elevation angles between +5 and +50° with respect to the horizontal.

SLADEN: How did you measure skin temperature?

COTE: Readings of external skin temperature were obtained by a thermistor mounted on a tension arm attached to the collar. The tension was calibrated to enable skin contact under normal activity conditions.

QUESTION: Do any of you object to using a harness?

CRAIGHEAD: Initially, we considered a harness but rejected it for a number of reasons. The elk really has a very strong neck. We didn't have many problems with collars reversing in the initial tests.

BULLOCK: There is a source of power that has not yet been mentioned. This is the piezoelectric source. Currently engineered devices obtain energy from the organism via its movements and produce about 1/5th or 1/6th of a mW power continuously with very high efficiency. It would be a negligible load for an ordinary bird in terms of extra work, to deflect a piezoelectric crystal to produce a milliwatt. The advantage is that you are getting away from any prepackaged foreign power source and are dealing with an endogenous source of power.

The device, for instance, which Carl Enger (ref. 13) has been using in dogs takes some of the work from the respiratory muscles which bend a small device, about 30 grams in weight, a cylinder about 50 mm long and 10 mm in diameter. The main element is a piece of ceramic which is deformed very slightly. This deformation produces the power—a relatively high voltage (around 20 V) at low current. From this particular device they are getting about 300 microwatts continuously.

What would be needed to increase the power to one milliwatt is another gram of weight increasing the bulk from 30 to 31 grams. This would add enough ceramic material so that about a milliwatt could be obtained continuously. The problem becomes where to attach the device. They are working now loose in the pericardium, deformed by the beating heart, and fixed to the vertebrae and ribs, deformed by respiratory movements. This puts the problem back to the biologist where it really belongs. There is essentially a negligible loading in respect to weight and to work.

The point is, that with this small a device you could radiate milliwatts continually and interrogate the animal every minute or every hour, instead of compromising with an interrogation once a week.

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SESSION III

Radar Tracking of Birds

Chairman, DONALD R. GRIFFIN

Tracking Radar Studies of Bird Migration

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RADARS HAVE NOW BEEN USED to study bird migration for more than two decades (ref. 1). The majority of these studies have been performed with search radars, designed to detect a maximum number of targets aloft. Tracking radars, on the other hand, are designed to detect and follow a single target and extract the maximum information from this one target. To accomplish this, tracking radar antennas produce a pencil beam of radar energy rather than the fan-shaped beam produced by search radars. Detection of the target to be tracked is usually accomplished by first rotating the antenna in a search mode. When the radar echoes are displayed on a plan position indicator (PPI), an image similar in appearance to that obtained with search radars is produced (see fig. 1).

The interpretation of the PPI is, however, quite different; while search radars are designed to detect all targets regardless of altitude, the PPI produced by a tracking radar will show only those targets that fall within

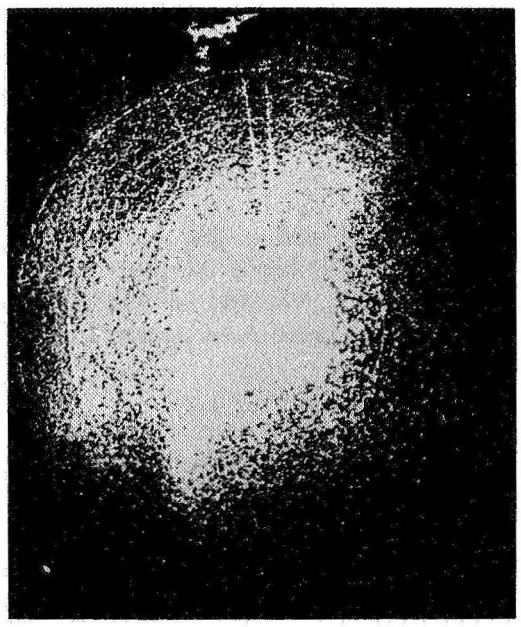


FIGURE 1. PPI presentation of SPANDAR radar, Wallops Island, Va., 1° elevation, 5-mile range marks. North is toward top of figure; coastline is oriented NNE to SSW through center. Major part of migration is over land to west of the radar.

its narrow pencil beam. Since this beam is usually directed upward, the altitude of targets will necessarily be a function of range. Bellrose and Graber (ref. 2) utilized this principle in their study of the altitude of nocturnal migrants. A number of other investigators have also used the pencil beam of small tracking radars (refs. 1, 3 and 4). Not until recently, however, has there been an effort to use the second stage of radar tracking, that of actually following a target once it has been detected in the search mode. Such studies have been performed by Gehring (ref. 5), Houghton (ref. 6), and, as is noted by Griffin and by Bruderer and Steidinger (this volume). Once the radar is set in the tracking mode the amplitude and modulations of the radar echo reveal the size of the target and most probably the wingbeat pattern (refs. 5 and 6). We hope that the analysis of such radar signatures will greatly aid in the identification of nocturnal migrants.

TECHNIQUES

The radars used in this study were the SPANDAR (and briefly the Q–6) radar at Wallops Station, Va., and the Q–6 radar at Bermuda. The radar characteristics are given as follows:

SPANDAR
- 10 cm (2700–2900 MHz)
- 5 Mw, peak power
- 18.3-meter (60-ft) parabolic dish antenna
- 0.39° beam width (at half power points)

Q–6
- 5 cm (5400–5900 MHz)
- 3 Mw, peak power
- 8.84-meter (29-ft) Cassegrainian parabolic dish antenna
- 0.40° beam width (at half power points)

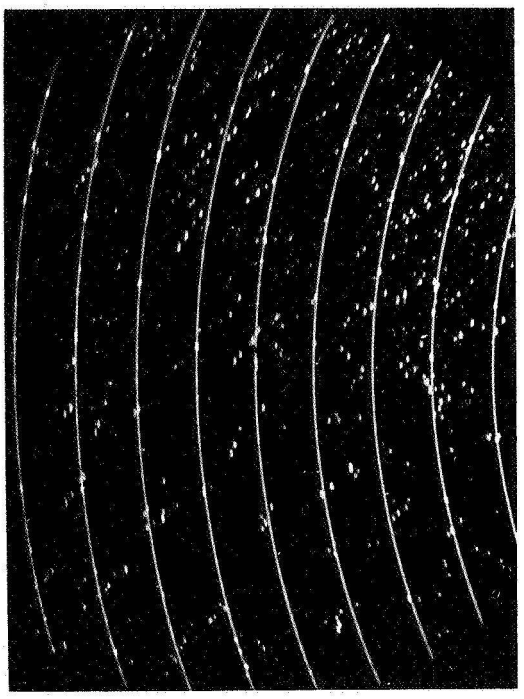


FIGURE 2. Sector scan of small area to west of the radar shown in figure 1 (2-mile range marks, 16- to 36-mile range).

Before tracking we used a polaroid camera to obtain photographs of the PPI display; these enabled us to assess the general patterns of migration and to determine the most profitable areas for tracking. Figure 1 was made during a heavy nocturnal migration over Wallops Island in April 1969; the shore line is oriented through the center of the figure running NNE to SSW. As one may see from figure 1, the major part of the migration at

FIGURE 3. Speed, direction, and present location of moving birds are recorded by timing the camera shutter action while photographing radar display; this technique was used in figures 1 and 2.

this time was over land. During such dense migrations, search radars are often saturated over much of their usable range and, as in the center portion of figure 1, individual targets cannot be distinguished.

Figure 2 demonstrates how the pencil beam of the tracking radar may be used to separate targets during even a heavy migration. The PPI display is off-centered covering the range from 26 to 58 km (16 to 36 mi with 2-mi range marks), the center of the sector scan being due west from the radar. Both figures 1 and 2 were made so that the direction and speed of the targets, as well as their position, could be determined. The radar was rotated twice with the shutter of the polaroid camera held open. The shutter was closed for the third revolution of the radar antenna and opened again for the fourth. All moving targets would thus show as two dots followed (in time) by a third at some distance, as illustrated in figure 3. Although individual targets can be distinguished only at the periphery of figure 1, figure 2 reveals that the migration over the Cheasapeake Bay was strongly oriented toward the NE; 78 targets were flying a course between 000° and 090°, five targets between 090° and 180°, and only four between 180° and 360°. Photographs such as figures 1 and 2 allow us to determine whether the bird tracks we obtain represent the typical flight direction and speed or an unusual type of movement.

The use of the pencil beam also allows one to determine the density of radar targets; the volume swept out by the radar beam in the central sector of figure 2 is about 220 cubic kilometers (54 cubic miles) if we assume the SPANDAR radar detected only targets within its 0.39° beam width. This would give a density of 1.6 targets per cubic mile. (If one wished to be more conservative and count only the largest targets, the density drops to 0.86/cubic mile.)

We used the PPI photos to select the most promising areas to obtain bird targets. This was done by specifying azimuth, elevation, and range, and then having the radar operator search for bird targets in that area. Bird targets were identified on the *A* scope[1] by their small size (relative to aircraft) and rapidly fluctuating amplitude. During the preliminary phases of our work, there is undoubtedly a bias toward the selection of large bird targets as these would be easier to track. Once an operator had set the radar to automatically track a target, we checked the target speed using an analog plot board; any target moving at more than 160 km/hr (100 mph) was rejected.

After accepting the target as a bird target, range, azimuth, antenna elevation, and average echo amplitide were recorded once a second on magnetic tape for later analysis. The analog plotboard was used for real-time analysis. In addition we maintained a continuous log of *A* scope observations, such as nearby targets and weather. If it appeared that the radar had swtiched targets during a heavy migration, we considered this to be a new bird track. At the beginning of each track and at 20-min intervals we obtained a 2-min record of the fluctuations in echo strength, and the azimuth and elevation errors of the radar for later identification of the target's radar signature.

After a relatively short period of time the SPANDAR operators became so skilled at tracking birds that we were able to briefly interrupt tracking, obtain weather information with the radar, and then regain the target for further tracking. The weather information consisted of radar images of cloud formations near the bird target. The radar was either moved to the right and left of the target (PPI) to determine the horizontal ex-

[1] Display of radar echo amplitude vs time.

tent of the clouds, or moved above and below the target to determine the altitude of clouds (RHI: range height indicator). This technique is illustrated in figure 4. This figure also illustrates the manner in which birds may avoid weather. Here, a bird is moving

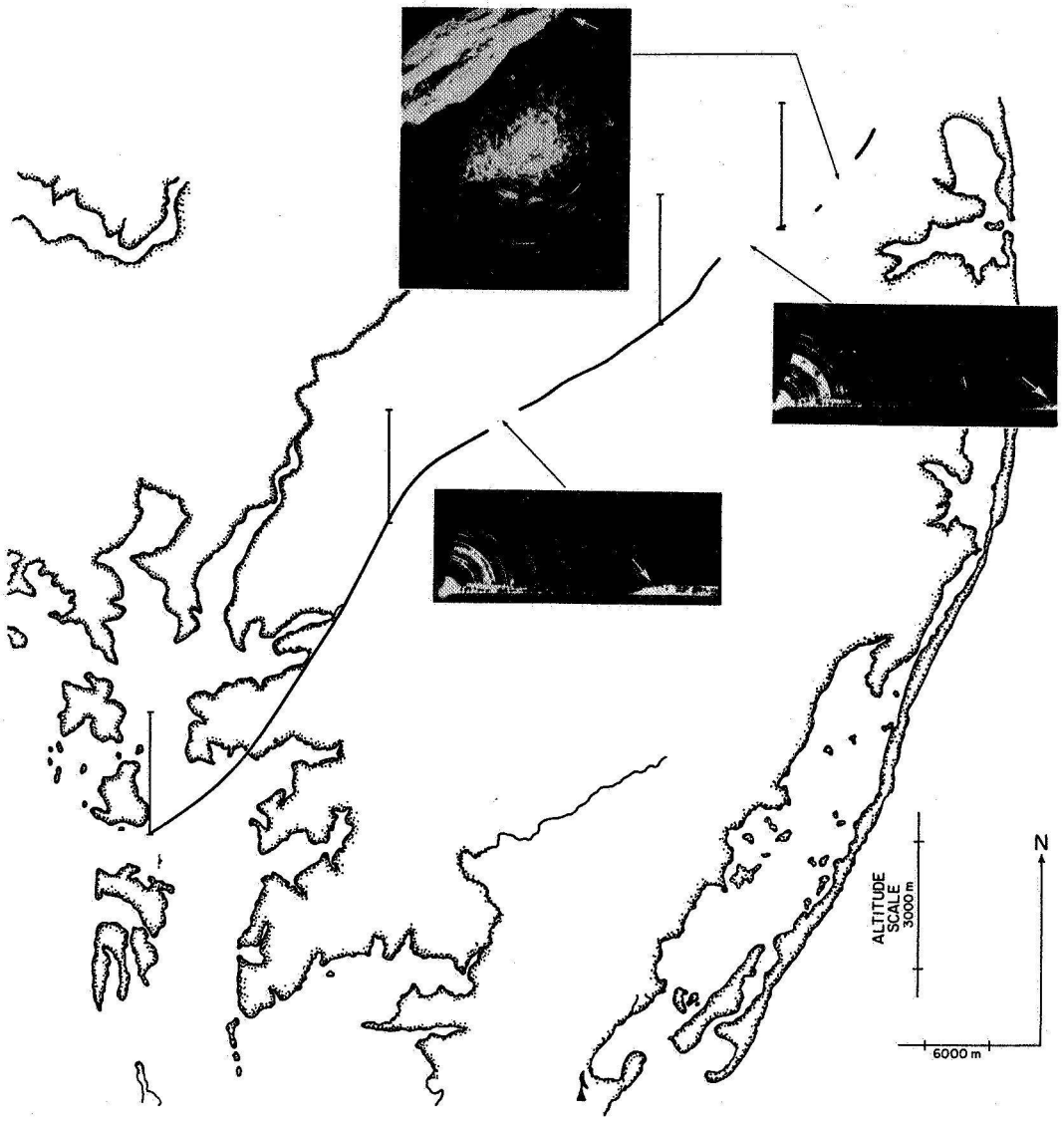


FIGURE 4. Track of bird avoiding heavy weather. Tracked from SPANDAR. Track was interrupted at three points to take PPI and RHI records of weather shown in insets; position of bird indicated by arrow. In some RHI's it was possible to have bird echo show in the weather photograph. Altitude at four points on track shown by bars and also on track 12K–L–M in figure 6. Bird can be seen above cloud front in RHI displays. Shape of track fits the shape of cloud front in PPI display.

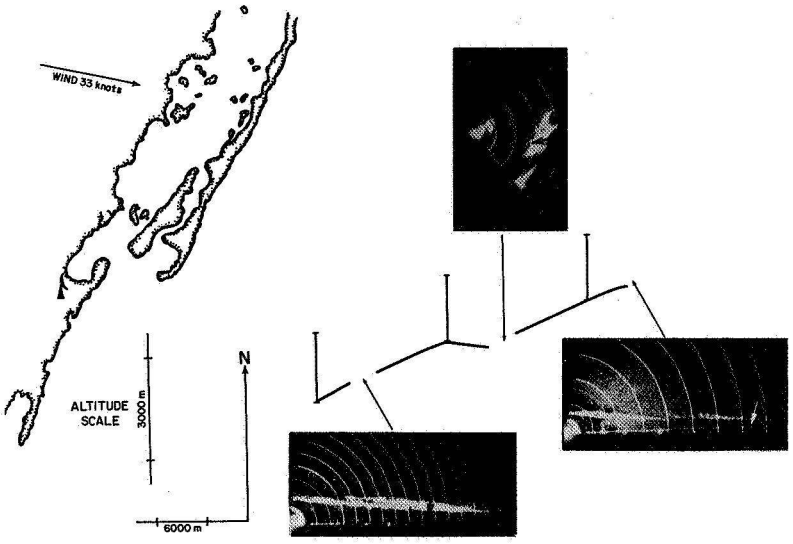


FIGURE 5. Track of bird flying beneath cloud layer over open water (SPANDAR). Track was interrupted at three points to obtain PPI or RHI weather data shown in inset; position of bird is shown by arrow. Pencil beam of this radar only picks up clouds above (beyond) target, although clouds extended on all sides for several miles.

along the edge of an advancing cold front. The two RHI insets, in which altitude is up and range to the right, show the bird just above the edge of the cloud bank. The PPI inset taken just before we lost the target, reveals that the shape of the advancing front closely resembles that of the bird's track.

Figure 5 illustrates another interaction of brids and weather—birds flying under a heavy overcast. In this case the two RHI insets show a dense layer of clouds above the bird; the PPI reveals that the clouds extend several miles on either side of the bird. (Note that the PPI only shows clouds beyond the bird; this is due to the pencil beam of the radar failing to intercept the high clouds at the altitude of the bird.) Tracks of birds on this night will be discussed later.

Analysis of the digital data consisted of a computer printout once every 5 seconds of elapsed time, speed of the bird relative to the ground, direction of flight, altitude of the bird with corrections for curvature of the Earth, rate of climb or fall, and radar crossection of the target. Plots were made of the x, y coordinates and altitude vs time. The minimum smoothing needed to eliminate errors in the tracking radars was used in these plots. One aim of our research has been to analyze the accuracy of bird navigation under a variety of weather conditions. In order to obtain an estimate of the straightness of the plots, we fitted a linear equation to the plot using the least squares method. The standard error of estimate (based on 500 points at equal time intervals along the track) was then computed for the following variables: East-West range (x) [vs North-South range (y)] and altitude (vs time). The interpretation of these standard errors will be discussed below.

Weather data consisted of surface observations, winds aloft from radiosondes at the Wallops Island and Kindley AFB (Bermuda)

weather stations, and satellite photographs of cloud patterns above the eastern coast of the U.S. and Bermuda.

RESULTS

During the spring of 1969 we were able to observe at the SPANDAR radar from March 24 through April 4 and from April 21 to 25. A second set of observations was made during the fall from October 6 through 17, using both the SPANDAR at Wallops Island and the FPQ–6 at Bermuda. Up to this point our work has been primarily exploratory, assessing the capabilities of the radar systems for following bird targets. The use of long-range tracking radars, however, has already added new data tc the study of bird migration.

Figure 6 presents all the tracks we obtained at Wallops Island under clear skies (both spring and fall) that were more than 60 km (200 000 ft) long. This figure gives the plots of altitude vs time as well as the vector computation of wind, air, and ground velocities for the targets. Inspection of figure 6 reveals several different types of tracks representing (we believe) different populations of migrating birds.

Tracks such as 9F–G–H–I and 5D during the spring and 15D during the fall correspond to our idea of the typical migratory bird track—a long straight track directed toward the presumed migratory goal. Other tracks such as 28H, 23A, and 30D are also long and straight but appear to be headed into the vastness of the Atlantic Ocean. As yet we cannot determine if a bird's course is appropriate to its destination, only its accuracy in maintaining course. Table 1 presents the standard error of estimate for the deviations of these tracks from a straight line. This is done first for the horizontal plot coordinates and then for the altitude of the bird's flight.

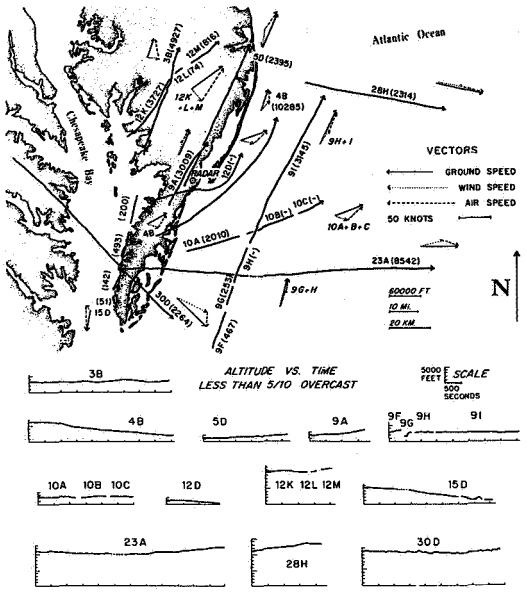


FIGURE 6. Bird tracks longer than 200 000 ft recorded under less than 5/10 overcast. Upper half shows the x-y coordinates of the tracks against local topography. Each track is identified by a number and letter followed by x-y standard error in parenthesis. Code number identifies the day of tracking (3–12, spring 1969; 15–30, fall 1969); letters distinguish tracks made on the same day. At various points along the tracks, vector diagram of wind, ground, and airspeeds is given. Winds were taken at radar site at altitude of the bird. Lower half of figure gives plots of altitude vs time for each bird track shown above. Breaks in the tracks were used to take RHI or PPI data on weather and other targets. Altitude data below 3000 ft may be unreliable due to anomalous propagation of radar beam.

The *x,y* standard error for most "straight" tracks is about 1 percent (The *x,y* standard error for all tracks obtained is presented later in this paper as a function of track length). The standard error of altitude reveals that many birds appear able to determine altitude with great accuracy. Track 3B maintained an almost level flight producing a standard error of only 56.7 me-

TABLE 1.—*Standard Errors of Straight Tracks (shown in figure 6)*

Track	Length (ft×10³)	x, y error [a]	% of length	Slope	Altitude-time error	% of length
3B	216	4.297	2.2	+0.019	0.186	0.085
5D	290	2.395	0.82	+0.336	0.077	0.026
9F	62	0.467	0.75	+1.452	0.034	0.055
9G	33	0.253	0.78	+7.497	0.190	0.58
9I	320	3.145	0.98	−0.283	0.052	0.016
10A	99	2.010	2.0	.....	.....	.....
23A	590	8.542	1.4	−0.373	0.110	0.019
28H	280	2.314	0.83	+1.223	0.116	0.041
30D	432	2.264	0.52	−0.116	0.281	0.065

[a] A linear equation was fitted to the horizontal track and to plot of altitude vs. time; the standard error of bird tracks with respect to the linear equation indicates the accuracy with which the birds could maintain altitude and course.

ters (186 ft) on a track 66 km (41 miles) long, and track 5D was able to maintain a steady rate of ascent within 10.4 meters over 88.5 km. Track 30D illustrates the track of a bird that was apparently able to maintain course but not altitude. The altitude plot shows periodic fluctuations of about 150 meters (500 ft) which are correlated with changes in forward speed suggesting soaring flight. As may be seen from the triangle of velocities in figure 6, this bird was heading at an angle of about 60° away from its actual track; yet despite this and its undulating flight, the bird produced one of the straightest tracks we have recorded.

Even on clear nights not all bird tracks were straight. At least one of these, 12K–L–M, we know to result from the attempts of the target to avoid an approaching storm (see fig. 4); track 9A may represent a similar circumstance. Some tracks in figure 6 show a constant decrease in altitude (4B, 12D, and 15D). This often occurred when birds were flying against unfavorable winds. The birds apparently descended to seek calmer conditions near the surface. Bird 4B was successful in finding a favorable wind, and 12D and 15D either landed or flew too low to be tracked. The shorter tracks we obtained (not shown) exhibited similar patterns to those shown in figure 6.

On any one night there was a definite tendency (which we have not yet quantified) for all targets tracked to be similar in heading (see discussion under PPI above), altitude, and speed. Our impression is that we were usually dealing with only a few types of bird movements on a given night.

Although dense clouds obliterated the radar echoes from bird targets, we were able to track on several nights when the sky was completely obscured by high cloud layers. Clouds were considered opaque only when surface weather observers reported 10/10ths cover before and after the period of tracking, when RHI photographs (as shown in fig. 5) showed heavy cloud layers, and when satellite photographs indicated that the clouds extended over large areas. Figure 7 presents all available tracks under such conditions. These data clearly show the ability of birds to maintain course even over open ocean without reference to the stars. The birds in figure 7 could, however, probably see the lights on

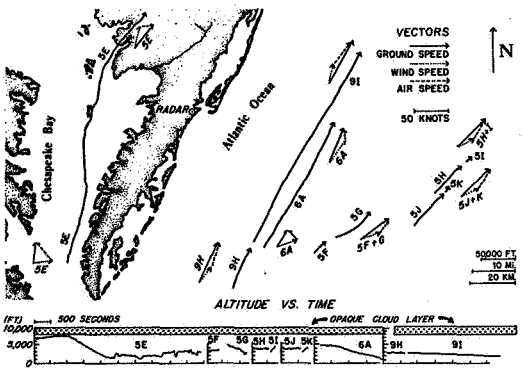


FIGURE 7. Tracks of birds flying under overcast, SPANDAR radar, symbols as in figure 6. Altitude of cloud layer shown by stippling on altitude plots.

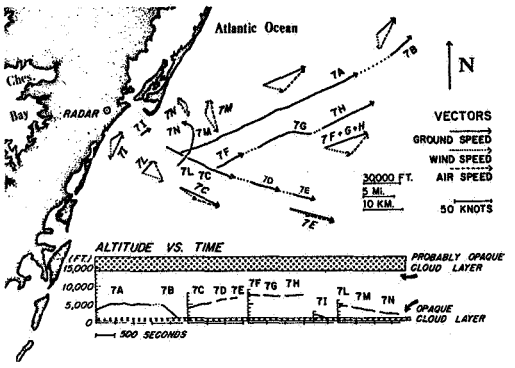


FIGURE 8. Tracks of birds flying between cloud layers. Symbols as in figures 6 and 7.

land. Track 5E is interesting in that solid overcast moved over Wallops Island about one hour before we began that track. At the beginning of track 5E, the bird was at 2100 to 2400 m near the cloud layer, and bucking a strong crosswind. Shortly after we began tracking, the bird descended rapidly (the rapid changes in altitude during the later part of the track may be due to anomalous propagation of the radar beam), and successfully maintained course despite having to change its compass heading more than 120°. The changes in course near islands and shorelines suggest the use of landmarks for piloting. Target 6A also descended and obtained more favorable winds without altering its true course despite a change in heading of about 60° (see vector diagrams in fig. 7). Since this bird was almost 48 km (30 mi) at sea, the use of landmarks is less likely than in track 5E.

On April 2, 1969, heavy fog or low clouds at about 180 m (600 ft) obscured the sky during our period of tracking. The RHI shown in figure 5 indicated a dense cloud layer at about 4.6 km (15 000 ft). Surface observations and satellite photographs before and after our tracking indicated that this was a totally opaque cloud layer. Thus, the birds tracked on that night were probably flying between layers of clouds without visual reference to either the sky or the earth. The tracks of these birds are shown in figure 8 with the exception of two very short tracks 7J and 7K. Track 7C–D–E represents the only case of birds flying with the wind that night; in all other cases the birds flew at some angle to the wind. The straightness of tracks 7I, 7C–D–E and 7F–G–H might be explained by the birds' flying at some constant angle to the wind, with the turn in track 7G being explained by a short downwind flight to avoid turbulence. But 7A–B and 7L–M–N cannot be explained in this way; these tracks clearly do not maintain a constant angle to the wind. Both the direction and speed of the wind in track 7A–B changed considerably as the target descended. The velocity of the bird relative to the ground also changed during the same period. The air velocity, however, remained remarkably constant both in direction and speed. This may be even more clearly seen in the case of 7L–M–N. The relevant data for this track are given in table 2. Thus, the tracks of these two birds may be best explained by the bird's maintaining a

constant compass heading without reference to the sky or land and despite shifting winds. The curves in the tracks would be due to the changing direction of the wind, the birds perhaps being unaware of the changes in their actual track.

In the fall of 1969 we made simultaneous observations at Cape Cod (Massachusettes) and Bermuda in addition to those made at Wallops Island. Figure 9 is a PPI photograph made on October 14 at the Q–6 Bermuda radar. The outline of the Bermuda islands can be seen to the left of the center due to anomalous propagation and echoes from sidelobes of the radar beam. The figure shows a strong movement to the SSE—120 targets heading from 120° to 180°, six from 190° to 230°, and four from 010° to 060°. These birds were not simply following the wind; in fact the wind on that night was from the East (see tracks 1B and 1C, p. 124). It thus appears certain that large numbers of birds actively cross the open Atlantic Ocean in migrations from North America to South or Central America. In the future we hope to correlate observations at several radars along the Atlantic coast with observations at Bermuda and Antigua (W. I.) to learn more about this migration route. In October 1969 we were able to observe only three strong migrations over Bermuda. Observations at Cape Cod indicated large numbers of birds departing from the Cape to the SSE between 28 and 40 hours prior to the appearance of large numbers of birds over Bermuda islands.

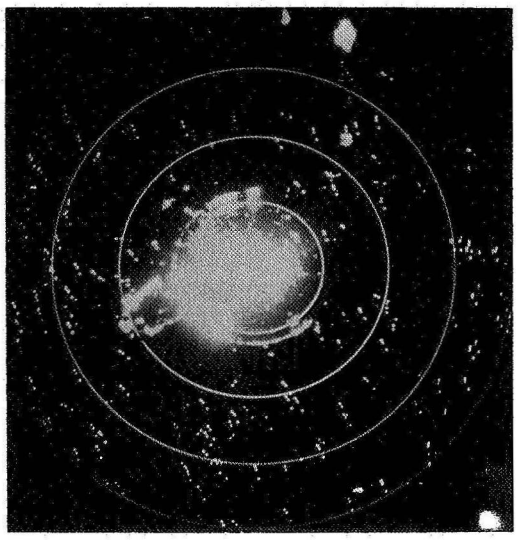


FIGURE 9. PPI photograph of birds migrating over Bermuda. FPQ-6 radar, October 14, 1969, 1745 GMT, 5-mile range marks, 1/2° elevation.

Figures 10 and 11 present all the tracks longer than 10 km obtained from Bermuda of birds moving south. As with birds moving over Wallops Island, the *x,y* standard errors are about 1 percent of the track length, and the altitude standard errors are about 0.1 percent of the track length. All tracks taken at Bermuda were made under clear or only partially cloudy skies. The straightness of the tracks does not appear to be correlated with either compensation for wind drift (compare figs. 10 and 11) or with level flight. Fig-

TABLE 2.—*Vector Analysis of Track L-M-N*

Vector	Direction of vector for track			Change in vector during flight
	L	*M*	*N*	
Wind	115°	140°	160°	45°
Track	40°	20°	300°	100°
Heading of bird	335°	340°	330°	10°

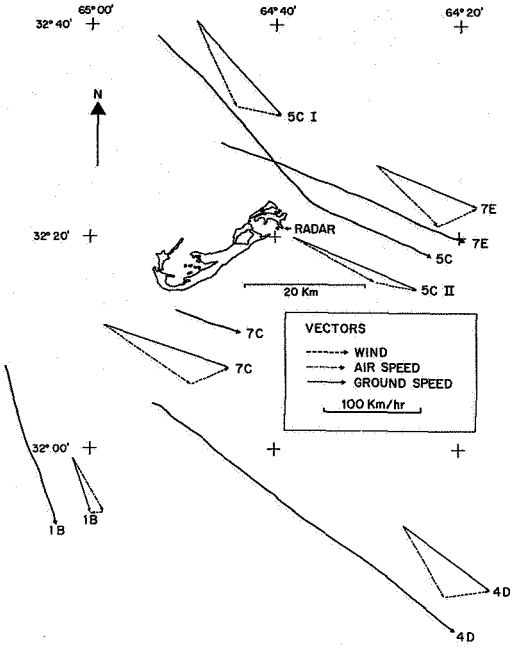


FIGURE 10. Tracks of birds migrating to the southeast across Bermuda. Symbols as in figure 6. Plots of altitude vs time not shown.

ure 12 shows the altitude plots for tracks 4C and 9E. Both birds were flying within 20° of the wind direction. Track 4C maintained altitude, and its x,y error was 917 m (3010 ft) or 4.1 percent of the track length. Bird number 9E, like other birds on day 9, produced a very irregular altitude plot (presumably due to turbulence behind a recently passed cold front), yet the birds on day 9 produced very straight tracks; the error for track 9E was only 177.4 m (582 ft) or 0.43 percent of the track length.

Figure 13 presents all the tracks longer than 10 km obtained at Bermuda that were not shown in figures 10 and 11. All these birds are moving eastward, but they are not being blown in that direction by the wind (see track 3A and 3B); they are actually flying a compass heading of between 100° and 120°. These courses even without wind drift would fail to intersect the South American continent. Thus, these birds appear to be actively moving to the east. Such movements are by no means uncommon; they were ob-

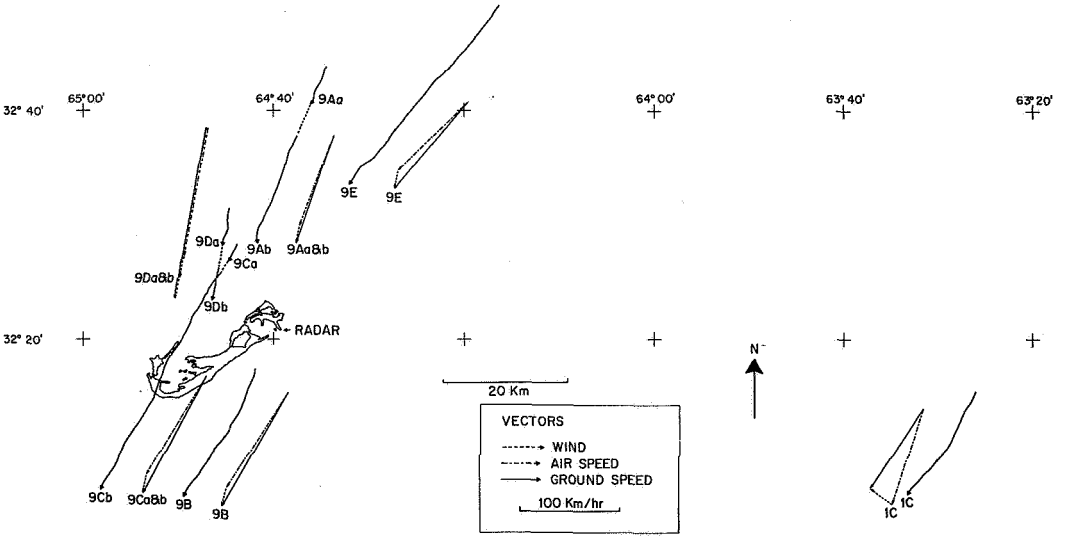


FIGURE 11. Tracks of birds migrating SSW across Bermuda. Symbols as in figure 6.

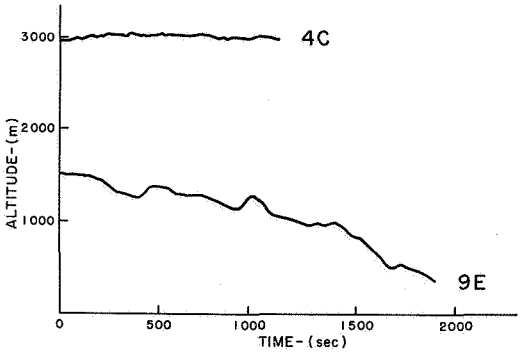
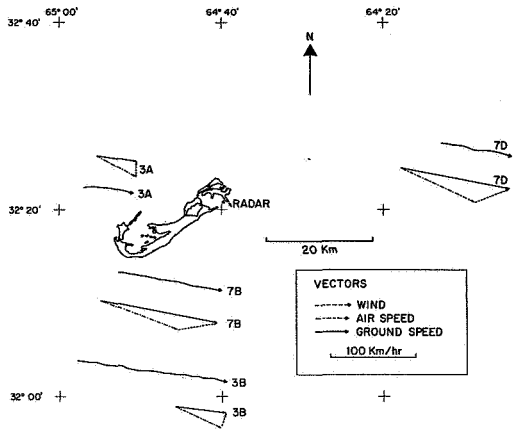


FIGURE 12. Plots of altitude vs time for two tracks of birds moving across Bermuda.



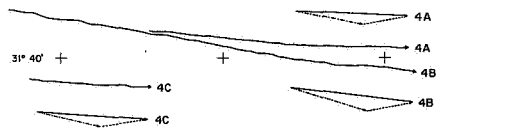


FIGURE 13. Tracks of birds moving east across Bermuda. Symbols as in figure 6.

served on 5 of the 9 days we were able to observe at Bermuda. At present these tracks, which might be continuations of tracks such as 23A and 28H in figure 6, represent a new facet of the study of bird migration: Is the navigational apparatus of these birds upset in some way or are they part of some new migration route either to Africa or, by an indirect route, to South America?

To date our principal findings are the ability of birds to maintain course under overcast skies and the movements of birds across Bermuda. If future data confirm our present results, it would appear that birds are able to maintain a compass heading by some means other than visual reference to the sky or Earth. It appears, however, that the birds cannot compensate for shifts in the wind without visual reference. Under these circumstances bird migration might be accomplished by maintaining a compass heading between checkpoints, either celestial or terrestrial. In this regard tracks such as 5C in figure 10, in which a target altered course as it passed near Bermuda, are most interesting.

In the future we hope to increase our knowledge of the radar targets in order to separate what we believe are distinct populations of migrating birds with different goals and perhaps different navigational techniques. Also we would like to know whether we are dealing with single birds or flocks that might pool their information. The radar crossection of the target is often helpful in the latter instance. The largest targets we have followed (with a crossection of 0.1 m^2) are certainly flocks while the smallest (with a crossection of 0.00001 m^2) are probably single targets. Another valuable tool in this effort will be the analysis of radar signatures (see also Bruderer and Steidinger, this volume.) Figure 14 presents the records of the automatic gain control (AGC) voltage which is proportional to the amplitude of the radar echo. In the upper portion of the figure, one may see the effect of increasing the number of birds in a target. A single brant gives an AGC record with regular fluctuations at about three per second; the azimuth and ele-

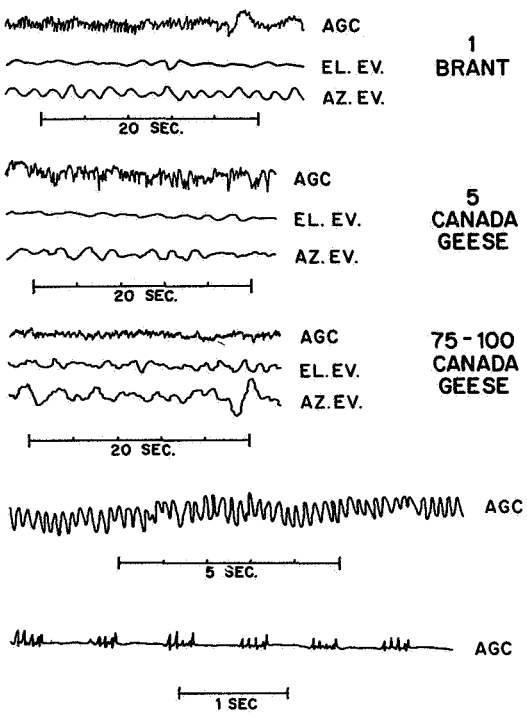


FIGURE 14. Radar signatures of migrating birds. AGC is output of automatic gain control, proportional to radar echo amplitude. EL. EV. is elevation error voltage, a function of vertical extent of the radar target. AZ. EV. is azimuth error voltage, a function of horizontal extent of the radar target. Upper part of the figure illustrates changes in radar signature with increasing numbers of birds in a target; lower part of figure presents two AGC records: the first presumably a waterfowl, the second probably a small passerine.

vation error voltages, also given in figure 14, are small and regular. A group of five Canadian geese no longer produces regular AGC changes, and the error voltages are irregular as the beam locks onto centers of density within the small flock. The record for 75 to 100 geese shows a great increase in irregularity in all parts of the records. (Absolute value of the AGC level should be disregarded here as it is a function not only of the target crossection but of the range of the target.) Of particular interest are the very large error voltages; visual observation through a boresighted telescope revealed that this was due to the radar "walking" between different targets within the large flock. The lower section of the figure illustrates the way in which we hope to identify birds by their AGC records. Although neither of these records were identified visually, the upper record is strongly suggestive of the wingbeat pattern of small waterfowl (regular at about 5 cycles/sec) and the lower might well result from the undulating flight of small passerines (a rapid burst of wingbeats followed by a short glide with wings folded). By identifying more signatures, we eventually hope to at least divide our targets into general groups of birds.

We hope to gain insight into the sensory mechanisms involved in navigation by analyzing the errors of tracks under different visibility conditions. Figure 15 presents all the available standard errors plotted against track length. A major diffiuclty at present is that the error is apparently a function of track length; in other words the tracks do not simply oscillate around a straight path. It may be that the errors are of two sorts—a small one representing the ability to maintain course and a larger error (more than 1000 ft) resulting from corrections of position or navigation. At present it is at least clear that there is no obvious difference in track errors under clear, overcast, or partially cloudy skies.

ACKNOWLEDGMENTS

We are especially indebted to Robert Krieger, Director of the Wallops Island NASA station, for his interest and help in the project. Gene Godwin of Wallops Island and Dean Bonnell of the Manned Space Flight Network bore most of the brunt of planning and organization for this research. In all

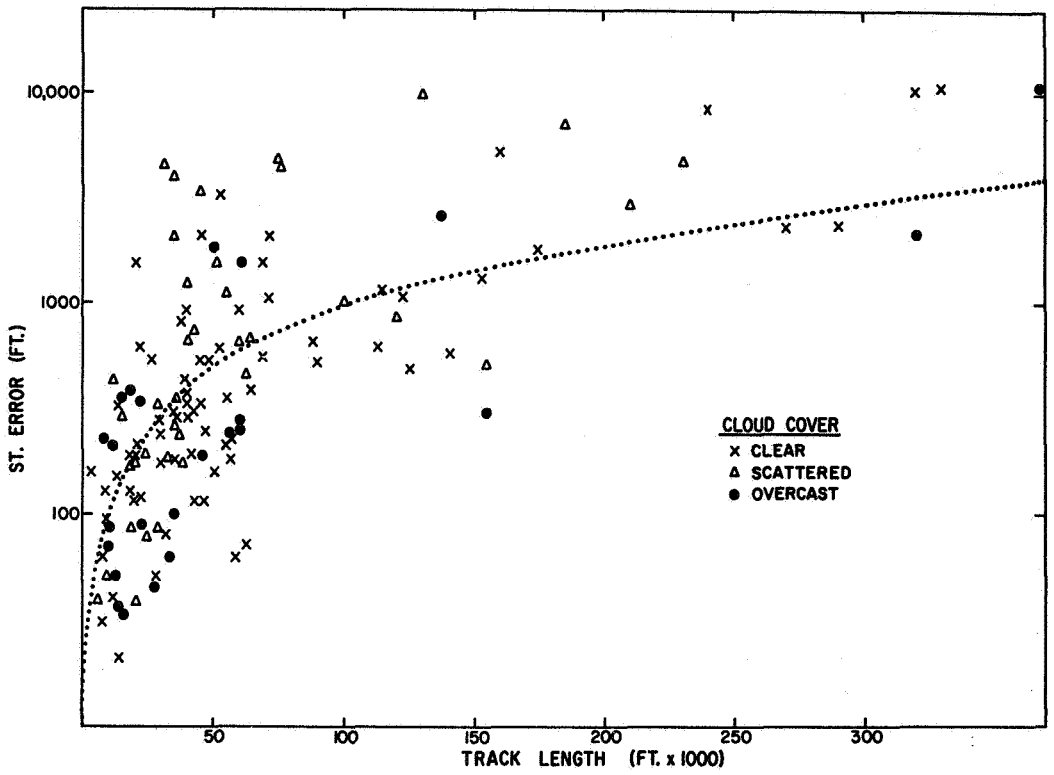


FIGURE 15. Plot of x-y standard error vs track length under three weather conditions as indicated. Dotted line gives level of 1 percent of track length.

phases of the work we were and are grateful for the help of both the radar and supervisory staff who have often gone far beyond the bounds of duty in helping us to understand and utilize the equipment.

The use of the radars and data analysis were generously donated by NASA. Funds for travel were provided by NSF grants GZ 259 and GB 13246 and Grant 508651F from the Research Foundation of the State University of New York.

DISCUSSION

WALCOTT: Did you see a greater number of birds on the upstream side of Bermuda and fewer on the downstream side, because of the birds coming in and landing?

WILLIAMS: Not for movements that went from north to south; in other words, the typical migration direction. But, on one or two days there was a difference--it looked as though there were more targets coming in from the west than were going out to the east. In general, we did not see too many landing. The birds that were seen on the ground represent a miniscule fraction of what was flying overhead, plus the fact that large numbers of the tracks and the PPI particularly showed no funnelling into Bermuda.

SLADEN: Are you sure you are tracking birds and not bats, gulls or butterflies? And if so, are you certain you are following the birds going out to sea from the mainland? Might they not have been normally feeding?

WILLIAMS: The analysis of the radar cross section of the targets that we tracked indicated that none of the targets were insects since they would be too small. Furthermore, our radar has the greatest skin tracking capability of any radar that I know.

The SPANDAR was used for insect tracking at a range of 1.6 km. We didn't try to track anything that near; 4.8 km was the nearest.

We have a few target signatures analyzed, but very few. As for gulls and so on, most of the targets are terribly high including track 28 H, which is one of those going out. The two straight ones going out to the east were both about 3000 m (10 000 ft). At that time the PPI display indicated large numbers of birds going out in the evening in that direction. We tried once to analyze the question—Do they come back?—by staying up all night. We found that they continue going out to the east all night long. They didn't turn around and come back; they were high; they kept on; and we didn't see them coming back.

My experience is that gulls and other shore birds are apt to be low flyers when they go out over the ocean. Furthermore, we see them coming in from the east to Bermuda.

COCHRAN: Where did you get your wind information for Bermuda?

WILLIAMS: At Kindley Air Force Base just a few miles from the radar. The winds aloft, in our case, were taken within 48 km of the bird, within 2 hours, and within 150 m (500 ft) of the bird's altitude. We also used the radiosonde to check the cloud layer.

BRUDERER: Have you eliminated dc outputs in your echo signatures?

WILLIAMS: No. That is the raw AGC level.

BRUDERER: What about low frequencies? I did not see slow changes of the AGC level, which we are used to seeing in our own echo signatures.

WILLIAMS: The low frequency is primarily due to changes in aspect and changes in the range of the target. We compute cross-sections by knowing the range and the AGC level. The low frequency changes were observed for soaring birds with large aspect changes, but for constantly flapping birds the aspect changes were minimal, which strengthens our ideas about the heading.

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Flight Directions of Passerine Migrants in Daylight and Darkness: A Radar and Direct Visual Study

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Clemson University

ON ALMOST EVERY NIGHT IN SPRING, migrant songbirds depart from regions south of the Gulf of Mexico, fly over the Gulf, and arrive on the northern Gulf coast during the daylight hours (refs. 1 and 2).[1,2] The migrants contained in these flights encounter a night/day transition while over the Gulf, and some of the migrants also encounter a subsequent day/night change before making a landfall on the northern Gulf coast. Still others alight on the northern coast during the day and, after a few hours, continue their journey after nightfall. These events present one with a unique opportunity to study the orientation of nocturnal migrants in daylight and in darkness.

MATERIALS AND METHODS

I collected radar and simultaneous telescopic data on 140 dates during the spring seasons of 1965 to 1967 and 1969 at the Lake Charles and New Orleans weather bureaus in southern Louisiana (fig. 1). These stations are equipped with the new WSR–57 radars. These sets are 10-cm radars of 500-kW power and have 2° beam widths. A pulse length of 4 μsec was used during the study; the set

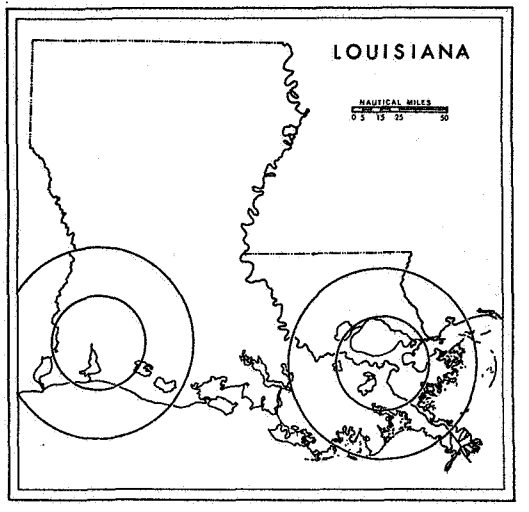

FIGURE 1. Map of WSR–57 radar surveillance areas at Lake Charles (left) and New Orleans (right) with circles delimiting 25- and 50-n. mi. ranges.

[1] GAUTHREAUX, S. A., JR.: A Quantitative Study by Radar and Telescope of the Vernal Migration of Birds in Coastal Louisiana. Unpublished Ph.D. dissertation, Baton Rouge, Louisiana State Univ. (Univ. Microfilms, Ann Arbor, Michigan. Diss. Abstr., vol. 29, no. 3538–B, 1968.

[2] GAUTHREAUX, S. A., JR.: A Radar and Direct Visual Study of Passerine Spring Migration in Southern Louisiana (in press).

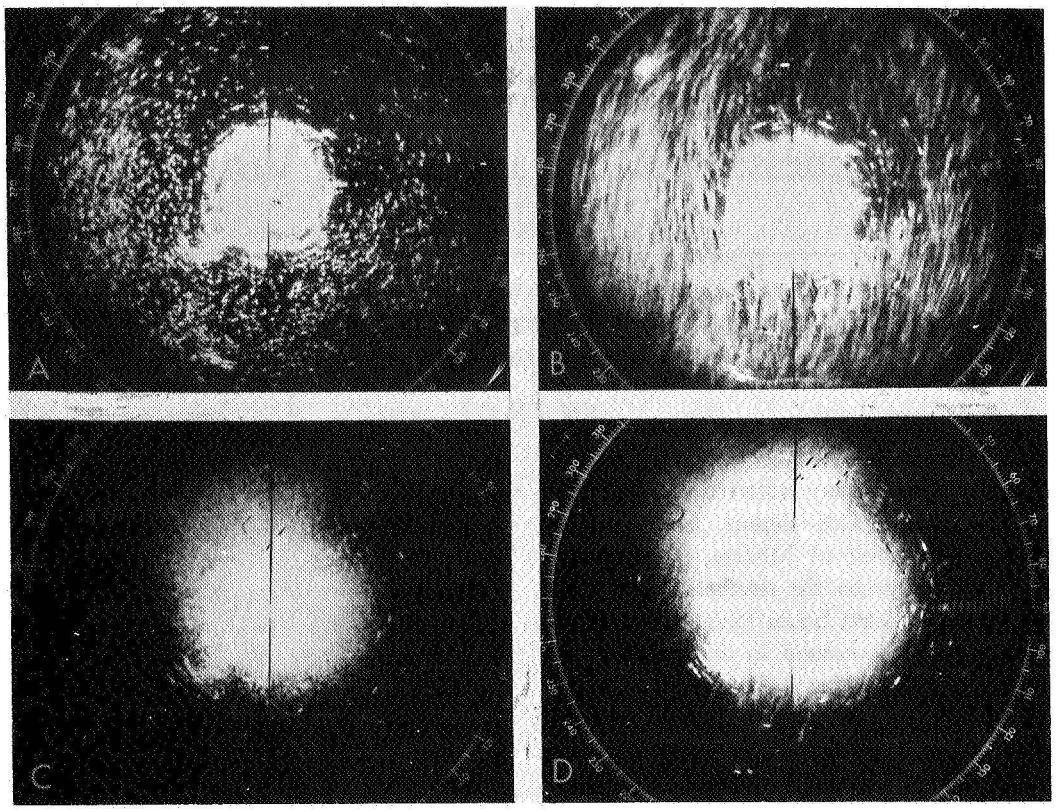

FIGURE 2. Radar photographs of migration taken at 3° antenna elevation on May 14, 1965, at Lake Charles, Louisiana (time is Central Standard). (A) 1347 hours, one revolution; (B) 1348 to 1353 hours, 15 revolutions; (C) 2010 hours, one revolution; (D) 2010 to 2015 hours, 15 revolutions. All photographs taken on 25-n. mi. range.

also has a 0.5-μsec pulse length. I collected most of the radar data on a 25-n.mi. range, but some data were gathered on 50- and 100-n. mi. ranges. I determined the altitude of the echoes from the range and elevation of the radar beam and from the range-height indicator (RHI). Additional characteristics of the WSR–57 radar appear elsewhere (ref. 3).

The methods for telescopic observations are essentially those described by Lowery and Newman (ref. 4). During the day the telecope was mounted vertically and a small portion of the sky above the observer was sampled. The 20-power ocular was normally used (field of 112 ft at 1000 yd), but a 30-power eyepiece (field of 78 ft at 1000 yd) was used when birds were flying very high. Occasionally I made brief vertical observations with 10 $\times$ 50 binoculars to supplement the telescopic watches. At night the telescope was trained on the Moon when the latter was visible and directed up a narrow beam of intense light (ref. 5) when it was not. Telescopic watches were normally made near the radar stations, but a few were made 19 to 24 km (12 to 15 mi) from the stations.

Before and after a period of telescopic observation, a single 35-mm exposure was made of the radar screen for one revolution of the antenna (20 seconds) followed by another photograph continuously exposed for 9 to 15 revolutions of the antenna (3 to 5 min). The short exposure was used to estimate the density of radar echoes; the long exposure was used to obtain information on the direction and speed of echo movement. Most of the photographs were taken with a 35-mm single lens reflex camera mounted on a tripod in front of the main radar screen. Kodak Plus X film (ASA 125) was used for most of the photography, but several Polaroid transparencies (46–L film) were taken of the remote radar screen.

I recorded all the available winds-aloft data from the weather stations surrounding the Gulf of Mexico. Radiosonde winds-aloft data (radar-tracked balloon) were gathered each day at 0600 and 1800 hr at these stations; pibal winds-aloft data (visually tracked balloon) were collected at 1200 and 2400 hr when cloud cover was above 1500 m (5000 ft). Local surface weather data for Lake Charles and New Orleans are available each day of the study.

RESULTS

Early in the study after examining the first few radar photographs, I realized that the echoes on radar from passerine migrants arriving from over the Gulf appeared to move with the wind at the various altitudes where the migrants were flying. Figure 2 illustrates this point. Figure 2A is an exposure for one revolution of the antenna; the dot echoes on this photograph are produced by flocks of passerine migrants. Simultaneous telescopic observations indicated that the flocks ranged in size from two or three to 175 birds, and the average flock size was 20 birds.

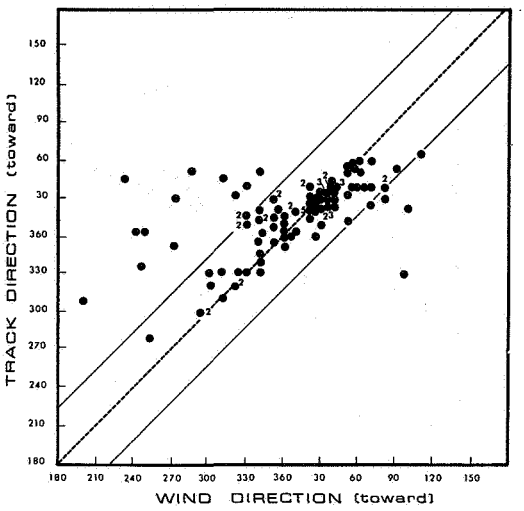

FIGURE. 3. Scatter diagram of daytime migration track directions and corresponding wind directions. Dashed line represents perfect agreement between track direction and wind direction; thin continuous lines delimit a 40° sector on each side of dashed line. *N* equals 106.

Some of the dot echoes are contributed by flocks of shorebirds. The change in track directions with change in altitude (and wind direction) is illustrated in figure 2B.

To further examine the relationship between track directions and wind directions, I compared the radar track directions of daytime migrants with simultaneous winds-aloft data for the spring seasons of 1965 to 1967 and 1969. Only track directions within 1 hour of the time of winds-aloft measurements are considered. Figure 3 shows the scatter diagram of daytime migration track directions and the corresponding wind directions. Each dot represents the track direction of migration on a particular date for a particular altitudinal stratum within an hour of a winds-aloft measurement. Eighty-six percent of the points fall within 40° of the wind direction. The remaining points indicate track directions that cannot be consid-

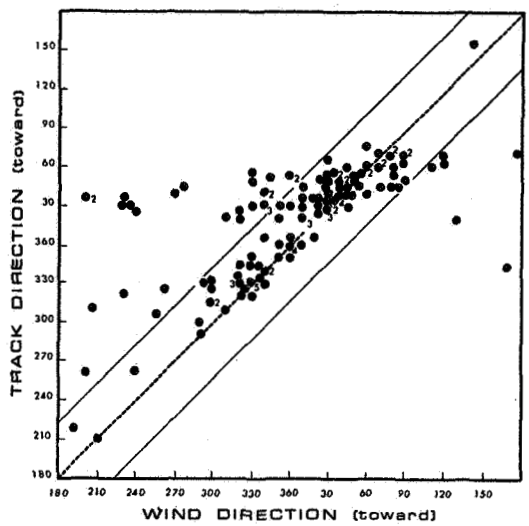

FIGURE 4. Scatter diagram of nocturnal migration track directions and corresponding wind directions. Dashed line represents perfect agreement between track direction and wind direction; thin continuous lines delimit a 40° sector on each side of dashed line. *N* equals 136.

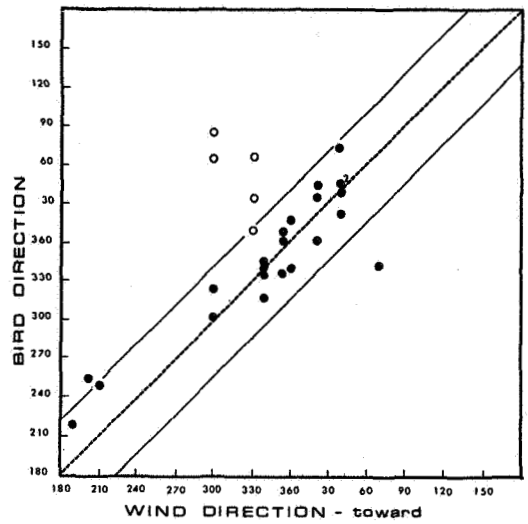

FIGURE 5. Scatter diagram of resultant vectors of nocturnal migrations and corresponding wind directions. Migration data gathered on 28 nights by ceilometer observations at New Orleans, Louisiana, during spring 1967. Open circles represent wind speeds less than 6 knots; solid dots represent wind speeds greater than 6 knots.

ered downwind. These latter points represent, with only two exceptions either very weak winds (less than 6 knots in velocity) or shorebird movements. Dot echoes on radar identified as flocks of shorebirds always moved at air speeds in excess of 25 knots in directions that were the same as the flight directions of the shorebirds that passed through the field of the telescope.

Figure 2 (C and D) shows the characteristic presentation of nocturnal migration on the radar screen. Figure 2C is an exposure for one revolution of the antenna; Figure 2D is a time exposure showing movement of the fine, grainy echoes produced by songbirds flying individually in the night sky. The scattered dot echoes in the misty pattern yield distinct streaks on the time exposures, and simultaneous Moon-watching and ceilometer observations indicate that the dot echoes are contributed primarily by flocks of waterfowl and shorebirds. Figure 4 is also a scatter diagram of bird track directions and the corresponding wind directions, but these data are for nocturnal migration. Seventy-six percent of the points fall within 40° of the wind direction. The remaining points fall beyond this zone, and as during the day these points are the result of light winds (more prevalent after dark) and strong flying shorebirds and waterfowl (airspeeds from 25 to 35 knots).

The relationship between wind direction and migration direction at night is further documented in figure 5, where the direction of migrations computed from ceilometer data and the corresponding wind data at 305 m (1000 ft) are plotted. Samples from 28 nights during the spring of 1967 at New Orleans, Louisiana, are represented. The migration directions are the resultant vectors computed

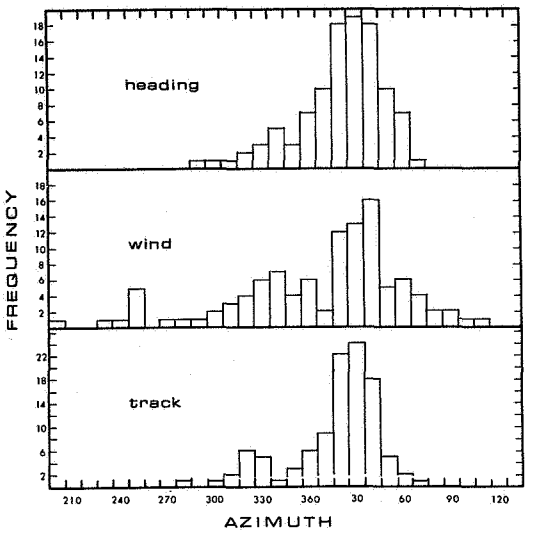

FIGURE 6. Frequency diagrams of heading, wind, and track directions for daytime migration. *N* equals 106.

from individual bird directions for a particular night's movement. The ceilometer data were gathered during the first two hours of darkness, and the wind directions are those for 1800 hr. In figure 5 winds of less than 6 knots are plotted as open circles; winds above 6 knots are plotted as solid dots. Seventy-nine percent of the points in the figure are within 40° of the wind direction. Only two solid dots appear out of this zone, but four of the five open circles are out of the 40° sector.

The frequency of track, wind, and heading directions during the day are illustrated in figure 6. The specifics concerning wind and track directions are the same as those given earlier in the text for figure 3. There is a tendency for track directions to vary less than heading directions, and this implies some correction for wind drift by the migrants. I found that shorebirds exhibited this ability during the day, and the flocks of passerines also maintained their "preferred" flight direction when unfavorable winds were less than 6 knots. In southern Louisiana, the wind most frequently blew in a direction that was quite favorable for the movement of spring migrants. In fact, the vast majority of spring migrants during the study did fly in the correct seasonal direction by simply flying downwind.

Figure 7 gives the track, wind, and heading directions for nocturnal migration for 136 observations during the spring seasons of 1965 to 1967 and 1969. The data presented here are the same as those given in figure 4. The spread in the directions of spring nocturnal migration is greater than that recorded during the day. At night the NW component of the migrations is more pronounced and is found at lower altitudes below 760 meters (2500 ft). Both the NW and NE nocturnal movements are downwind at their respective altitudes. In contrast to the daytime migrations, reverse migrations or flights in an inappropriate direction for the season are present at night, and some of these occur under clear skies.

When trans-Gulf migrations continued to

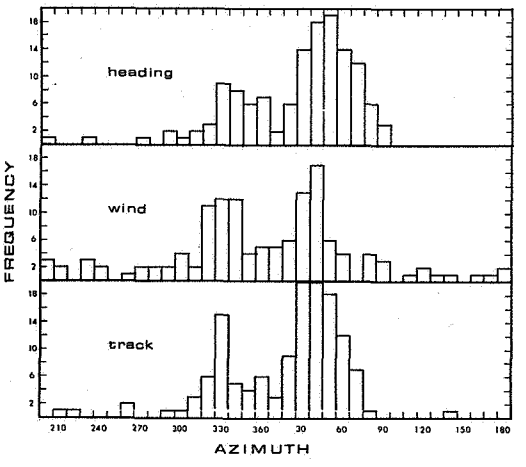

FIGURE 7. Frequency diagrams of heading, wind, and track directions for nocturnal migration. *N* equals 136.

arrive after dark, the flight directions did not change from the daytime flight directions independent of changes in wind direction. On 10 occasions trans-Gulf migrations moved inland in the afternoon to the northwest with strong winds from the southeast; the migrants that continued to arrive after dark did not change their direction at nightfall but continued flying to the northwest.

The trans-Gulf migrants that alighted in the woodlands of southern Louisiana during the daytime arrival of a flight departed 30 to 45 min after dark. As the migrants left the woodlands, their flight directions were oriented to the NW, but as they gained altitude the directions changed to N and then NE. In southern Louisiana during the months of April and May the winds below an altitude of 450 m (1500 ft) usually blow to the NW; between 450 and 900 m they blow to the N and NNE; and above 900 m the winds usually move to the NE and ENE (National Summary of Climatological Data, United States Weather Bureau, 1965, 1966, 1967, and 1969).

Isobars are lines on a weather map connecting points of equal barometric pressure. The wind blows nearly along isobars at 600 to 900 m above the ground. On April 25, 1965, the isobars over the central, northern Gulf coast were oriented from 120° to 300° at 1200 hours, and the movement of birds in from over the Gulf at this time was directed to 300°. Between noon and midnight the orientation of the isobars changed 70°, and they were oriented from 190° to 10° at midnight. The arriving trans-Gulf migrants showed a corresponding change in their flight directions, and those that continued to arrive near midnight moved toward 10°.

During the study 19 percent of the 106 daytime observations were made with solid overcast skies, and 14 percent of the 136 nighttime observations were conducted with solid overcast skies. In no case were the directions of these migrations different from those under clear skies. The migrations that left the woodlands of southern Louisiana under overcast did so without delay and with no noticeable deviation from the regular departure direction under clear skies.

DISCUSSION OF FINDINGS

Lack (ref. 6) stated that radar observations fit best with the view that migrants in flight orient solely by a Sun compass or a star compass since they do not, so far as can be determined, allow for lateral displacement by the wind (unless flying very low). Bellrose and Graber (ref. 7) have reported that their radar data show that birds compensate only partially for drift. Evans (ref. 8) and Nisbet and Drury (ref. 9) have concluded from their observations with radar that birds compensate exactly and continuously for drift. These authors also point out that migrants tend to fly with favorable winds thereby reducing their chances of drift. Bellrose (ref. 10) has stated that migrants generally select winds that are favorable for their goal, but when forced to use unfavorable winds, they correct to a high degree for lateral drift. Lack (ref. 11) subsequently re-examined his wind-drift data and concluded that his findings also support the ideas that birds select favorable winds and that they can correct for wind drift.

Steidinger (ref. 12), working with radar in northern Switzerland, found that radar tracks of migrants were clearly deflected by strong crosswinds, and concluded that birds apparently do not compensate for the drifting effects of the wind or only to a small extent. My findings support the drift hypothesis for songbirds, but it appears that strong flying shorebirds and waterfowl can correct for lateral displacement by the wind provided

the wind velocity is not too great. I have recorded several cases of downwind flight under clear skies when the wind was blowing in a direction that was inappropriate for the seasonal advancement of the migrants.

Lowery (ref. 2) found a striking correlation between air currents and the directional flight trends of birds, suggesting that most night migrants travel by a system of pressure-pattern flying. Evidence that birds select winds blowing in a preferred direction has been obtained by Bellrose and Graber (ref. 7), Gauthreaux [3], Evans (ref. 8), and Nisbet and Drury (ref. 9).

Several authors on the basis of their radar studies of migration have reported that birds initiate migration under overcast and are able to pursue a flight in the normal direction of migration without reference to solar or stellar cues (e.g., refs. 7, 9, 13). My findings support the claims of these authors and suggest that wind direction is a possible alternative to solar and stellar cues when overcast skies prevail.

The correlation between wind direction and the direction of migration suggests that most passerine migrants fly with the wind or, to express the matter differently, the wind often blows in the same direction as the direction of their migration. Since the average monthly wind directions are frequently the same as the preferred direction of the migrants, the birds often fly with winds that require no compensation for wind drift. Occasionally some day migrants maintained preferred tracks, even though the winds varied considerably from tail winds. Why birds flew with the wind in certain cases and at various angles to the wind in other cases becomes explainable when one examines the types of migrants involved and the wind speeds. Shorebirds, particularly the larger species with airspeeds from 25 to 35 knots, are not drifted by unfavorable winds of light to moderate strength to the same extent as are smaller, slower passerines (ref. 14). Passerines in flocks arriving from over the Gulf during the daylight hours did not drift noticeably when the winds were less than 6 knots. With stronger winds the passerine flocks drifted even though in many instances the birds had a clear view of the ground below them. Although most of the data presented in this paper and its figures are from radar echoes interpreted as passerine birds, some contamination by echoes from shorebirds and waterfowl is likely. This contamination would tend to give false support to the idea that passerines constantly correct for wind drift while migrating aloft.

I have shown that flight directions of the migrants aloft will often coincide with the wind directions at the various altitudes where the migrants are flying. The migrants are either selecting the altitudes where the winds are favorable, or the birds are being drifted from a standard direction by shifts in wind direction at various altitudes. One cannot determine what is happening without adequate knowledge of the migratory goals of the species involved. Myres (ref. 15) has reported that Scandinavian thrushes over the North Sea and North Atlantic at dawn show a behavior that he has termed the "dawn ascent." Reorientation of flight direction accompanies this behavior. Although I have not examined the winds-aloft information to support my stand, I do think it possible that the reorientation response by the migrants is probably influenced by a change in wind direction as the migrants gain altitude.

Basically the findings of this study support Pennycuick's (ref. 14) assertion that cross winds of moderate strength deflect slow birds

[3] GAUTHREAUX, S. A., JR.: Bird Migration as Simultaneously Viewed by Telescope and Radar. Master's Thesis, Louisiana State Univ., 1965 (unpublished).

through a large angle, but have less effect on faster ones. In general, the slower (and hence smaller) the bird, the more it is affected by unfavorable winds. The influence of wind direction on the flight directions of migrants should be taken into consideration in future orientation studies of birds.

ACKNOWLEDGMENTS

I wish to thank the personnel of the United States Weather Bureaus at Lake Charles and New Orleans, Louisiana, for their constant cooperation and assistance during the research. George H. Lowery, Jr., and Robert J. Newman kindly assisted me during the phase of this work that was used for a portion of my Ph.D. dissertation. I thank Kenneth P. Able for his help in the preparation of the manuscript. A portion of this work was completed under a grant (70–1879) from the Air Force Office of Scientific Research.

DISCUSSION

QUESTION: How do you correlate radar targets and visual identifications? You quite frequently distinguished between passerine and shorebird targets.

GAUTHREAUX: Moon-watching and ceilometer observations gave me information on the types of birds, their flight directions, approximate altitudes, and spatial distribution. I used these characteristics to identify the bird echoes on radar (e.g., intense dot echoes above 1500 m moving at an airspeed of 40 kt to the northeast corresponded to flocks of shorebirds and ducks at high altitudes flying to the northeast; smaller dust-like echoes below 700 m moving to the northwest corresponded to small and medium sized passerines flying to the northwest).

QUESTION: How high is your visual capability?

GAUTHREAUX: It varies during the day depending on atmospheric conditions. With a 30-power telescope I have seen birds when radar showed that the flight was entirely above 1200 m. These birds appeared very small and were near the limit of visibility.

WILLIAMS: I have done experimental work with a similar radar and also with a search radar at Otis Air Force Base in Cape Cod. My criticism is that you see a particular pattern of migration close to the radar and a different pattern of migration at some distance. Because of the elevation radar, you assume that the close pattern of migration is a low altitude one and the other is a high altitude one. I have also seen the same thing with a search radar. You mustn't forget that small targets will only be detected near the radar set itself. Search radar is presumably picking up all altitudes up to 3000 m (10 000 ft) including ducks and geese detected at great ranges and passerine birds moving in quite different directions at close range. Yet I wouldn't like to make any statement about altitude since I know that the small targets are detected at a closer range. Have you made any attempt to correct for that?

GAUTHREAUX: The small dust-like targets on the WSR–57 appear restricted to the center simply because of the antenna elevation and the low altitudinal distribution of the small and medium passerines at night. When I lower the antenna to 0°, the radar can detect these fine targets out to 50 to 60 n. mi. The pattern shrinks closer to the center of the screen as I raise the antenna. Thus, I am missing the small targets at 15 n. mi. because the 2° beam, when tilted 3°, starts to go above the bulk of the passerine migrants at that distance.

WILLIAMS: Another general question and perhaps criticism . . . of all the work done on wind drift, the general tendency is to use the average heading of the birds using the M.T.I. wedge. Other people generally tend to take the average heading of the birds and compare that to the average track. In my work I have found that even with a good and clear M.T.I. wedge I can get a spread of 50° with the actual tracks.

Have you tried looking at your data when you actually plot the track for each individual bird? If you do take the average as shown on PPI's, do you actually have a number of birds going in a totally different direction?

GAUTHREAUX: It is nearly impossible to analyze individual tracks of the numerous fine, misty echoes on the WSR–57 radar at night, but the ceilometer data can be easily analyzed in that manner. The angular deviations in tracks during a night of observation are normally on the order of 30 to 40° for the ceilometer. True, it is often misleading to talk of migration directions in terms of resultant vectors. When a low altitude movement is going to the northwest and a high altitude flight is moving to the northeast, the resultant vector will indicate a northward migration. This is largely meaningless. There is an advantage to simply plotting the raw data and looking at the grouping and total dispersion of the tracks.

QUESTION: I wonder if the paradox on wind drift corrections might not be a reflection of the physical condition of the birds themselves? Could some of these drifting birds be just very tired birds?

GAUTHREAUX: That is certainly possible. Tired birds might fly slower, and if so, their track would be deflected more by an unfavorable wind of constant speed. However, if fatigue is responsible for drift in migrants flying over land, why don't the birds land? I believe that the birds are in good health, are maintaining a constant preferred heading, and are being displaced by the unfavorable wind. Their track is the vector resultant of their heading and airspeed and the wind direction and its speed.

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Information on Bird Navigation Obtained by British Long-Range Radars

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IN THE YEARS 1958 to 1963 several British ornithologists were permitted to make observations of bird migration with surveillance radars of the Royal Air Force. These radars were superseded by more modern equipment in the early 1960's and access was then terminated. Thus the data used in this review refer to a period of observation nearly 10 years ago, though the analysis and interpretations are recent.

The radar equipment was a 10-cm surveillance antenna of the type described by Eastwood and Rider (ref. 1). It was of high power, such that a single "echo" from birds often could be tracked for 150 km and sometimes for over 200 km. Echoes were displayed on a plan position indicator (PPI) and records were made either directly from the display or by time-lapse photography (ref. 2). No moving target indicator facility was available. My own observations were made at a site in Northumberland, northeast England, in the autumns of 1961, 1962, and 1963 and in the spring of 1963.

Certain limitations of long-range radars are recognized in assessing the observations of birds in flight. The major disadvantage is large pulse volume. All reflecting objects within the pulse volume contribute to a single echo on the radar display. At about 60 km from the antenna, the pulse volume is the product of an area of resolution of about 0.67 km^2 with an altitude range from the ground to an altitude above the normal level of bird flight. Thus, a single echo on the radar display can correspond to any number of birds, depending on density and flocking behavior of migrants. At longer ranges, resolution of the radar deteriorates. Nisbet (ref. 3) has used this relationship to extrapolate simultaneous counts of echo densities at different ranges to derive a value at zero range, where resolution is greatest. By comparing this density with the migration density derived from counts of birds passing a siting of the Moon on the same night, he was able to calculate an average number of birds per radar echo and quantify the radar observations. Similar quantification was not possible where I was in northern England because of cloudy skies. Thus observations reported in this paper refer to numbers and directions of movement of echoes and not of single birds.

Findings relevant to the problems of bird

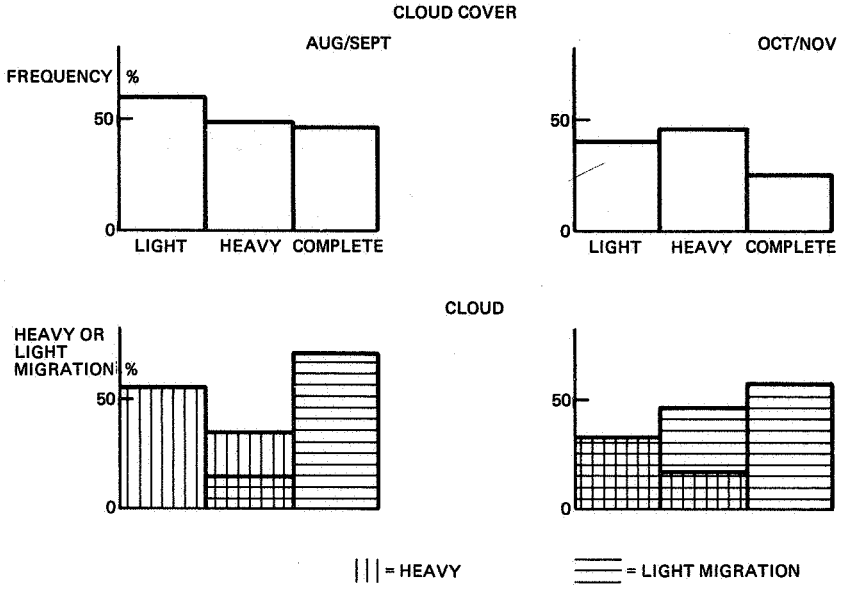

FIGURE 1. Relation between intensity of cloud cover and frequency and density of SSE migrations of passerines in northeast England, 1961 to 1963. Frequency of migration is given as percentage of nights with the particular weather condition on which migration actually occurred. Densities of migration are given as the percentage of nights of actual migration when heavy or light movements, respectively, were recorded. (Heavy + medium + light migrations = 100 percent).

navigation were: migration under total overcast; compensation for wind drift; reorientation after displacement; reversed movements; and changes in direction of flight during migration. These findings will be discussed using observations of passerine movements to the SSE in the fall and to the NNW in the spring.

MIGRATION UNDER TOTAL OVERCAST

Complete cloud cover was recorded over the area covered by the Northumberland radar on 42 of the 193 nights of observation in the autumns of 1961 to 1963. On 12 of these nights, rain echoes obscured the radar display of any bird echoes there might have been. Migratory departures were seen on 17 of the remaining 30 overcast nights. Thus birds were not deterred from setting out on migration under total overcast, although fewer did so on such nights than on clear nights (fig. 1). As soon as birds could be detected by radar they were correctly oriented, though it is not known whether they were flying above, in, or below the cloud layer. On several nights the birds departed under total overcast, with fog at ground level; landmark orientation would have been impossible on these nights. Further details are documented by Evans (ref. 4).

A similar picture is given by radar observations of passerines in the spring of 1963. Of 22 nights of total overcast, rain echoes filled the display on four nights. Migration was seen on 12 of the remaining 18 nights. Two departures were observed through fog at ground level. Departures of migrants under

complete cloud cover have been recorded for shorebirds as well as for passerines (ref. 5). These observations suggest that orientation by the stars is not the only method available to night migrants.

COMPENSATION FOR WIND DRIFT

From analyses of night-to-night variation in the mean direction of autumn migration, I concluded that both passerines and waders compensate in flight for wind displacement and fly on preferred tracks rather than on standard headings (refs. 4 and 5). This conclusion was based on four lines of argument:

(1) The night-to-night variation in track direction was less than in headings. This was true both in August and September when the chief migrants were warblers and chats, and in October and November when the chief migrants were thrushes.

(2) The mean track direction on nights when the winds blew from the right of the tracks was almost identical with the mean track when the winds blew from the left of the tracks. This finding held for the two groups of passerine migrants and for movements of shorebirds.

(3) The heaviest migrations did not take place with directly following winds, when track and heading would have coincided. On the five nights of heaviest migration in August and September of 1961 to 1963, wind drift was such that birds were blown between 25 and 80 miles away from their headings for every 100 miles they flew. Thus it seems unlikely that birds were trying to maintain preferred headings.

(4) The mean direction of migration did not change during the night, even when the direction of the upper-air winds changed by as much as 110°. This was true on five nights in September and another five in October and November, so that the finding applied to both groups of passerines. (Details are given in ref. 4, tables 6 and 10.)

The conclusion—that birds compensate for wind drift—is in agreement with the findings of Nisbet and Drury (refs. 6 and 7) and Bellrose (ref. 8) in America, but contrary to Lack's (ref. 9) original interpretation of his radar observations in eastern England. Lack's observations were interpreted again, independently, by Evans (ref. 4) and Nisbet and Drury (ref. 7). They based their interpretations on a model that required birds to compensate for drift in flight; but the model predicted that a larger proportion of migrants whose intended tracks were wind-assisted would depart on a given night, as compared to the proportion of birds whose tracks were partly opposed by the wind. Further details of this "selective departures" hypothesis are given in references 4 and 7. Lack (ref. 10) has reanalysed his data, and now agrees that birds keep to chosen tracks under most wind conditions.

The implications of this conclusion need to be considered. Perdeck (ref. 11) has suggested that young starlings (*Sturnus vulgaris*) reach their winter quarters on their first migration by a "direction and distance" process. The ability to keep to a chosen track direction in flight, as demonstrated above, would seem an essential attribute. But so also is an ability to measure distance. How might this be done?

The simplest method would appear to be flight for a predetermined time, but the distance traveled in a fixed time could vary widely with wind conditions unless a bird could hold its groundspeed constant. This implies that it would vary its airspeed. Yet Pennycuick (ref. 12) has shown on theoretical grounds that there is a certain airspeed that should be maintained by a bird of a given species and known weight if that bird is to achieve maximum flight range in still air. (A

bird's weight decreases as its fat reserves are used up during migration, and its cruising speed must also decrease to maintain maximum range speed.) If a bird adopts this strategy, then its groundspeed will be the vector sum of cruising speed and wind. Hence flying for a fixed time will not enable birds to fly a chosen distance.

In practice, however, recent radar studies by Schnell (ref. 13), Bellrose (ref. 8), and Bruderer and Steidinger (this volume) show that birds of several species seem to maintain more nearly constant groundspeeds than would be expected under a variety of wind conditions. Schnell's data, however, do not refer to birds on migration. Therefore, his findings are not unexpected, since Pennycuick's calculations show that the cruising speed for sustained migratory flight is only one of a range of airspeeds of which they are capable for flights of much shorter duration.

Bellrose's observations warrant further discussion. He found that the groundspeeds of migrants were not influenced in proportion to the favorable component of the wind force, and concluded that migrants reduced their own efforts as windspeed increased. He noted this phenomenon even on single nights, when the effects of different windspeeds presumably were examined by choosing birds flying at different altitudes and in different directions. His method of analysis—plotting the regression of groundspeeds of migrants against appropriate wind forces—is valid only if the same bird species may be found flying at any chosen altitude or under any wind conditions. I suspect that this condition does not hold. An alternative way of expressing Bellrose's conclusion is that at high (following) wind forces, the mean airspeed of the migrants recorded in flight is lower than that of birds flying at low wind forces. This might come about as follows: Birds probably choose the altitude and wind conditions in which to fly—so that migrants with the lowest cruising airspeeds might fly only with a large favorable component of wind force, whereas migrants with higher airspeeds are prepared to fly with less favorable winds. In a single migratory flight this might lead to a stratification of airspeeds with altitude, so that birds with low cruising speeds flew higher (to gain larger favorable components of the wind) than those with higher cruising speeds. Such stratification could be reinforced by the need for birds with higher cruising speeds to remain at lower altitudes to maintain adequate oxygen intake.

Until such possible alternative explanations of Bellrose's observations have been discounted, I remain skeptical of the possibility that a migrant's groundspeed is maintained relatively constant in a variety of wind conditions. Hence, I am still doubtful that a chosen distance can be achieved by flight for a chosen time. In any case, if birds conform to Pennycuick's predictions and always fly at maximum-range airspeed, the distance traveled in one hour by any bird will depend on its initial weight, which will vary during the course of migration.

Distance flown might also be measured by the rate of loss of fat reserves, but this rate depends on the power requirements of the bird, which in turn are affected by the problem of constancy of airspeed discussed above. Hence, loss of fat is a poor index of distance traveled. If distances are to be measured reasonably accurately by a juvenile bird migrating to winter quarters, there seems no easy way other than by comparison of coordinates of the starting and finishing points. (The hypothesis could then be made that when the distance so calculated equals an internally programmed distance, migration in that direction should terminate. Alternatively it should terminate when the migrant reaches a point whose coordinates are inherited—in

which case no distances need to be calculated.)

To return from his speculation, a direct consequence of the method a bird uses to compensate for wind drift is that there are certain wind conditions when compensation becomes physically impossible. Normally a bird heads somewhat into the wind to maintain its chosen track. If the wind is opposed to this track and is stronger than the bird's normal cruising speed, then a bird trying to compensate will be blown backwards. I have suggested elsewhere (ref. 4) that even before the speed of an opposed wind reaches the cruising speed of the bird, a migrant may allow itself to be drifted from its preferred course. The consequences of drift from the normal migration route will now be examined in a "natural experiment" in Western Europe.

REORIENTED MOVEMENTS

In August and September of 1961 to 1963, there were no regular migrations of passerines from Scandinavia to northeast England, as seen by radar. Yet in these same months every year, SSW movements of passerines are often seen by radar some 320 km farther south, in East Anglia (refs. 14 and 15). I believe these to be the western fringe of direct migration from Scandinavia to Iberia, though I am aware that many migrants probably leave Scandinavia in a more easterly direction (see, e.g., refs. 4, 16, 17). Under certain weather conditions, particularly with strong SE (opposed) winds, this western fringe of migrants can no longer hold its SSW course, and birds have no option but to be blown westward. They then alight in considerable numbers on the coasts of northeast England and eastern Scotland. Among the most numerous species are redstarts (*Phoenicurus phoenicurus*), garden warblers (*Sylvia borin*), and pied flycatchers (*Ficedula hypoleuca*), all of which are typical Scandinavian species; most of the birds are juveniles.

The fate of these birds, blown off-course, is of considerable relevance to ideas of how young birds reach their correct winter quarters in the absence of parental guidance during migration. Perdeck (ref. 11) has shown that young starlings, when displaced artificially from their normal migration route, fly parallel to that route. If the wind-displaced Scandinavian migrants did the same, i.e., flew SSW from northern Britain, they would fly out over the Atlantic and be lost. It seems, however, that in practice they compensate for their westward displacement and reorient toward their correct migration route. They do this even though they fly singly (ref. 18) and without calling in flight at frequencies audible to human ears; it seems, therefore, to be within the capacity of individual juveniles to reorient. The evidence for reorientation is threefold:

(1) Recoveries of displaced birds caught and banded in northern Britain come from the same parts of France and Iberia as those of birds caught in southern England during pauses on their normal migration. Furthermore, the percentage of banded birds subsequently recovered is the same for displaced birds of a given species as for undisplaced birds. Full details are given by Evans (ref. 16).

(2) When tested in orientation cages in northeast England, all but one of the displaced migrants which showed clear orientation did so in a direction eastward of their presumed original direction of SSW. They had thus compensated for westward displacement. Some compensation would have arisen merely if their internal clock had remained in synchrony with the longitude from which they had been displaced. But since they

moved westward no more than 15° of longitude, the maximum shift of their preferred orientation would have been 15° eastward, i.e. from SSW to just west of south. In fact, all shifts recorded were greater than this (ref. 16).

(3) After a very heavy arrival of Scandinavian migrants in northern England on August 31 and September 1, 1963, all departures of these birds (on the nights of September 2 and 3) were seen by radar to be indistinguishable in direction from the SSE mean direction taken by departing British migrants (ref. 4). While there was a spread of directions about this mean of SSE, all tracks lay east of south, implying that birds had shifted their heading eastward, and by more than the 15° shift discussed above.

In summary, the directions of reorientation shown by these displaced migrants would have taken them back to their migratory routes before they reached the areas in Iberia where banded birds were recovered. It is not known where rest and feeding areas for Scandinavian migrants are located in southern Europe. (Perhaps there are no specific areas, but each migrant rests and eats where it can, prior to the trans-Saharan crossing.) Hence the significance of the departure directions detailed above cannot be interpreted at present in terms of headings toward definite staging areas on a migratory route.

As an alternative to reorientation toward an intermediate staging point, whose coordinates the bird must know, Matthews (ref. 19) suggested that a bird might derive a reoriented direction by vectoring its standard direction of migration (at the time and origin of displacement) with the direction joining the origin to the point of arrival after displacement. To obtain accurate reorientation, the bird would have to measure distances accurately, and I believe this can be done only by comparison of coordinates, as discussed earlier. We do not know, however, how accurate reorientation really is. Hence an evaluation of the two possible mechanisms of reorientation cannot be made at present.

REVERSED MIGRATIONS

On several autumn nights, the migration seen by radar was in a direction exactly opposite to that expected, i.e., birds flew NNW instead of SSE, and no movement could be detected in the normal direction.

An analysis of weather data for the 17 reversed movements seen in the autumns of 1961 and 1962 revealed the following relationships:

(1) The surface winds on all nights were less than 10 knots, and from between SE and SW. They were thus opposed winds for normal migration. Yet normal SSE movements occurred on 52 percent of nights with light opposed winds in August and September, and 36 percent in October and November during the study period (fig. 2).

(2) Temperatures at 1800 hours, close to the time of departure, were very close to the long-term norm for the days of observation. (On only one night was the temperature more than 1°C above normal.)

(3) Cloud cover was complete on only three of the 17 nights; on another six nights, cloud cover was less than half.

(4) On five occasions, reversed movements occurred on two nights in succession.

In summary, these movements were not disoriented, nor always downwind, but rather were oriented along the correct axis of migration, though in the wrong direction for the time of year. The reversal of direction was not associated with atypical temperature at the time of departure, a feature which might have explained why all migrants agreed in choosing the wrong flight direction.

A possible explanation of reversed move-

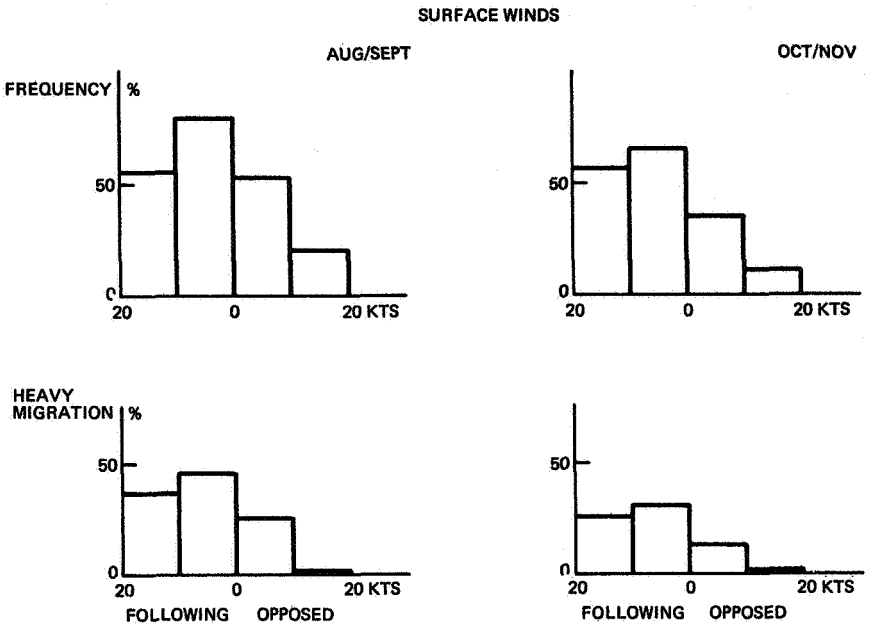

FIGURE 2. Relation between surface wind strength and direction and frequency and density of SSE migrations of passerines in northeast England, 1961 to 1963. Frequencies and densities are expressed as in Figure 1.

ments could be found if Rabøl's (ref. 20) hypothesis is established. Rabøl has suggested that the migratory route of a bird from its breeding grounds to its winter quarters can be thought of as the time-programmed movement of a "goal" area, so that on any chosen date during migration the migrant should be at a particular locality. If, for some reason, it had overshot this locality on a previous day's flight, then the bird might be expected to reverse its direction of flight to regain its correct (intermediate) goal, appropriate for that date. I am unhappy with this suggested explanation of reversed movements (even if Rabøl's hypothesis withstands test), as it seems most unlikely that a complete migratory flight (rather than few individuals) would overshoot the goal on a particular night, and thus be required to reverse their migration direction on the following night.

A further puzzle is that Emlen (ref. 21) believes that the choice of direction along the spring/autumn migratory axis is determined by the internal physiological state of the bird. By photoperiod manipulation he brought two groups of indigo buntings (*Passerina cyanea*) into the physiological states of spring and autumn migration, respectively, at the same time of year. When tested simultaneously under the spring planetarium sky, birds in spring condition oriented northward, those in autumnal condition southward. This experiment is, however, open to an alternative explanation: that the seasonal direction of migration is determined by the direction of the daily change in photoperiod. The birds Emlen brought into spring migratory condition experienced increasing photoperiods before their orientation was tested; those brought into autumn condition experienced

decreasing photoperiods. This suggests a hypothesis (as yet untested) for the occurrence of reversed migrations—that actual daylength on the date of the reversed flight was in some way different from those on previous days. More specifically, in autumn, I hypothesize that the daylength on the date of the reversed flight would be measured by the birds as being longer than on previous days (rather than shorter, as would be expected). This could result if a clear morning followed several days with cloudy mornings. Alternatively, since there is a circadian rhythm of photosensitivity (ref. 22), light intensities at particular times of day might be important.

Clearly the phenomenon of reversed migration requires further attention from radar ornithologists.

CHANGES IN FLIGHT DIRECTION DURING MIGRATION

Most of the small passerine night migrants which leave England in autumn are seen by radar to depart in directions east of south. Yet many species later reach Western Iberia, SSW of England, as shown by recoveries of banded birds. I have argued that the SSE departure direction allows migrants to fly partly with the wind on many nights when the same wind would be opposed to a direct SSW track (fig. 3). The migrants must change direction toward the west somewhere in southern France, allowing them to reach Portugal where they rest and eat. Although this may also require them to fly into the wind, the westerly winds in southern France are less strong than those in Britain. (The reason is that Britain is closer to the track of the low-pressure weather systems.) Hence the demands on a migrant are less (ref. 4). Also, movement into a headwind would take place overland instead of across the Bay of Biscay, so that a tired migrant could land safely, if necessary. In summary, the migration routes taken by many species seem to be a compromise between the need to reach a stopping area by the shortest way, and the need to avoid migration into strong headwinds if a preferred track is to be maintained.

In contrast to the large number of recoveries of banded passerine migrants in Iberia, very few recoveries of the same species have been made in the area where they are thought to change their direction of migration. Hence it seems probable that they do not need to land to change their course. This suggests that their map-sense is operative in flight. Further documentation is given by Evans (ref. 4).

It has been assumed in the foregoing discussions that birds fly along compass directions rather than along great circle routes. For chiefly north-south migrations, a migrant would save an insignificant distance by following a great circle route. However, for long east-west migrations, the great circle route would be preferable, e.g., at latitude 60° a 5000-km journey along the line of latitude could be shortened by more than 350 km by great circle course. However, to follow the latter course the migrant would need to change its compass heading continually, and this seems unnecessarily complicated unless it is performed incidentally, as a consequence of the method of navigation used.

CONCLUSIONS

The observations reviewed in this paper give more information on orientation processes than on navigation itself. For example, the migrants' ability to compensate for drift by the wind means that they are able to maintain an orientation in flight (but it tells us nothing of the way in which the orientation is first established). The unknown way in which drift is detected, and corrected for,

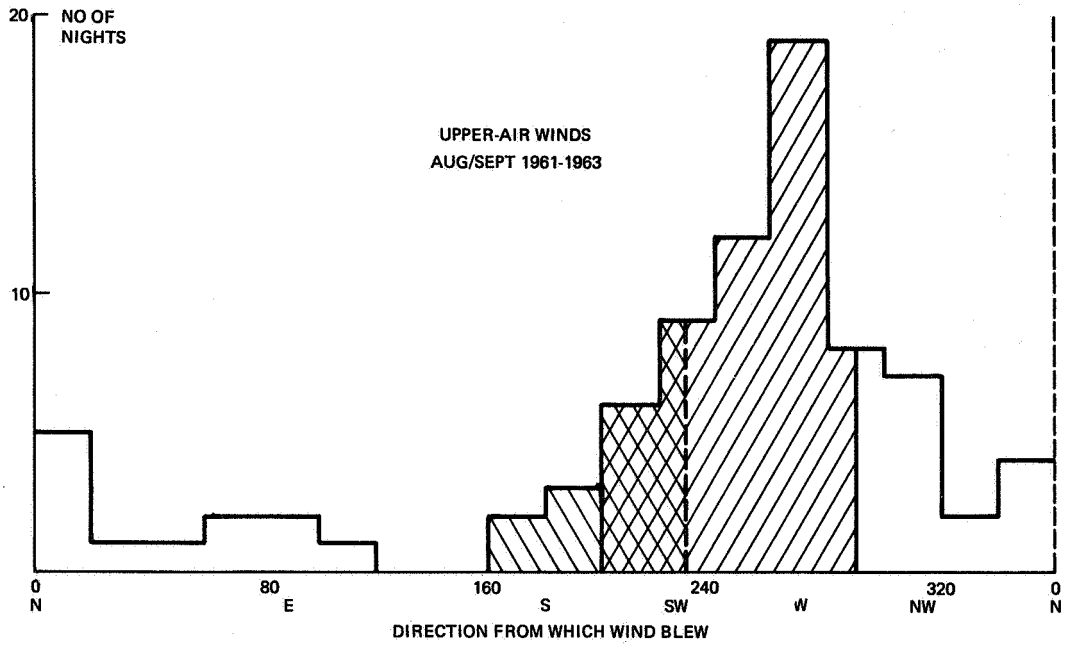

FIGURE 3. Distribution of upper-air (915 m) wind directions in August and September 1961 to 1963. Predominance of westerly winds is clearly shown. Winds from between SSW and WNW are opposed to a direct SSW flight from northern England to Iberia. By departing in a SSE direction, migrants convert a large proportion of these winds into partly following winds.

may or may not be related to the methods of long-distance navigation.

It seems clear that migrants are able to use more than celestial cues for orientation, as shown by the regular departures under total overcast and even through fog at ground level. Furthermore, the first journeys of certain long-distance migrants are more complex than the simple direction-and-distance movements demonstrated for starlings. Reorientation after displacement occurs; it is not known whether the new headings chosen by the migrants are indicative of their ability to navigate to an intermediate goal on the migratory route, or whether the new headings represent compromises between the standard direction of migration and the displacement directions. Insofar as navigation may take place by a map-and-compass process, it would seem to be used in flight, since changes in the direction of migration probably occur then. But radar studies have given no indication of the nature of the coordinate system used.

DISCUSSION

WILLIAMS: How did you identify the different groups of birds? You said some were waders (shorebirds) and some were passerines.

EVANS: Three methods were used to separate these groups—their times of departure, the departure localities, and their flight speeds. Waders departed between 1 and 2 hr before sunset from a limited number of coastal localities, well known as resting places for these species in northern Britain. Passerines departed from the whole land mass about 30 to 45 min after sunset. In August and September the mean flight speed of passerines was about 20 kt, whereas waders flew at over 30 kt; the

radar echoes from wader flocks were also much brighter than those from passerines. (Echo and flight speed differences between waders and passerines were much less in October and November and were not used to characterize the groups.) Details of species involved in the migrations are given in references 4, 5, and 16.

BRUDERER: Did you calculate the mean of individual headings on each night? Wouldn't the spread in individual headings be greater than in tracks on a single night?

EVANS: In my attempts to establish whether birds correct for wind drift, I worked with average track directions, assessed visually from the time-lapse films. From these I obtained an average heading for each night flight, by allowing appropriately for the wind velocity. I then compared night-to-night variation (spread) in average track directions with night-to-night variation in average headings. I am aware that Eastwood (ref. 23) has shown that on a single night, even if birds are drifted from preferred headings, the spread in resultant tracks can be less than in the headings. However, as I pointed out in my review of his book (ref. 24), Eastwood's analysis is irrelevant to the night-to-night comparisons made by several radar ornithologists, including myself.

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Methods of Quantitative and Qualitative Analysis of Bird Migration with a Tracking Radar

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THE AIM OF OUR WORK with a tracking radar was not primarily orientation research, but a study of intensity and height of migration under the influence of changing weather conditions and an examination of the different groups of birds and other animals involved in these migratory movements. Nevertheless we think that a presentation of the methods we have developed and of some of the results attained may be a valuable contribution to this symposium, because of their possible application in orientation research.

The present paper is based on two observation periods of three weeks each (March 19 to April 10, 1968 and April 3 to 25, 1969) in northern Switzerland near the Zurich airport (~ 430 m above sea level). In the first part of the paper we describe our method of assessing the rate of bird passage and discuss three topics—the grouping of nocturnal migrants, their velocity of flight, and the identification of species by radar echoes. Finally we will deal with height and volume of migration under different weather situations. The second part outlines the methods of studying the directions of migration and discusses the correlation between winds and the height and direction of migrating birds.

Part I by B. Bruderer

RADAR EQUIPMENT AND ITS APPLICATION

The equipment used in our studies (fig. 1) was a fire-control radar of the type "Superfledermaus" (produced by Contraves AG, Zurich) with a wavelength of 3 cm and a peak pulse power >150 kW. The narrow pencilbeam and extremely short pulse length allowed us to localize the smallest birds with an accuracy of a few meters in all three dimensions and to track them to ranges of more than 4 km. Further technical details may not be given because of military security.

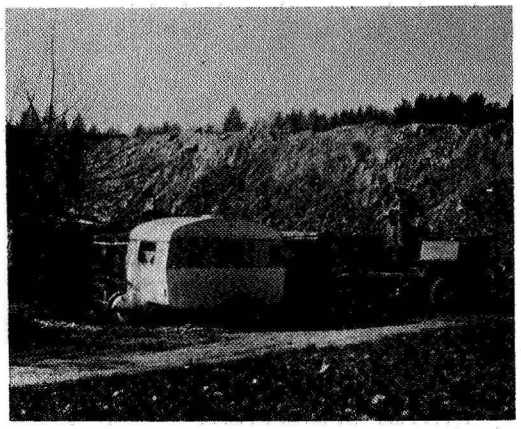


FIGURE 1. By operating the tracking radar "Superfledermaus" in a hollow, ground clutter may be avoided without applying MTI circuits.

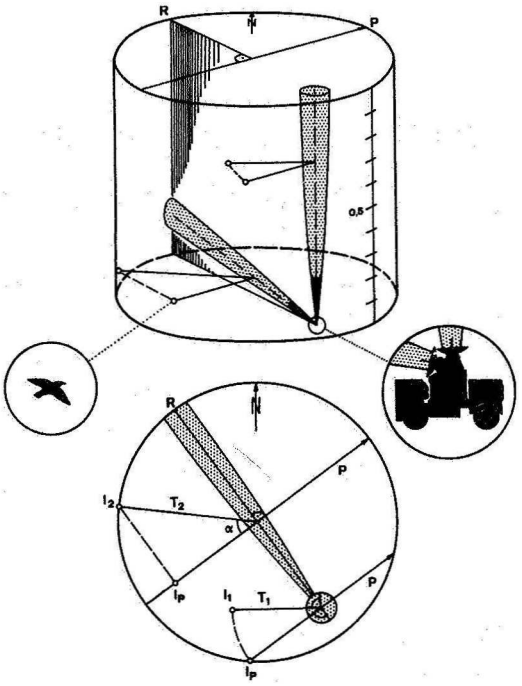


FIGURE 2. Principle of improved vertical-beam method: Beam is pointed vertically upward in the first phase, so ranges up to 4000 m above ground could be surveyed. Levels next to the ground are surveyed in second phase with low antenna elevation. Graph above shows volume of a cylinder with a height of 1 km and the radar site to the SE. Diagram beneath is the ground plan for the figure above. In both drawings *P* gives the supposed principal direction of migration and *R* is the plane of registration for low-elevation counts. Small circles mark position of single birds: I_p marking an individual with principal direction; I_1 and I_2 are individuals with the track directions T_1 and T_2. α is angle between actual and supposed migration direction.

One of the most important conditions for ornithological work with a tracking radar is a suitable site in a hollow, which reduces ground clutter. The application of moving target indicator (MTI) circuits is not recommended because birds that fly at low speeds (against the wind) will often be eliminated (ref. 1). We employed two main techniques: quantitative and qualitative. The qualitative methods inform us about direction, speed, and height of automatically tracked targets; simultaneous recording of AGC-signals (voltage of the automatic gain control) gives us the possibility of analyzing the echo signatures produced by these targets. The quantitative methods inform us about height and volume of migration.

QUANTITATIVE METHODS

The basic technique of our quantitative measurements was an improved vertical-beam method (fig. 2). The narrow beam, widened by conical scanning, was pointed vertically upwards for 20 minutes. In a second phase the beam was directed at low elevation perpendicular to a supposed principal direction of migration (~55°) over the edge of the hollow. It was thus possible to reach birds flying as low as 30 m above ground. Objects crossing the beam could be counted on the A-scope (range indicator) and were registered according to their ranges. The A-scope trace could also be displayed on a separate oscilloscope in Z-modulation (i.e., in-

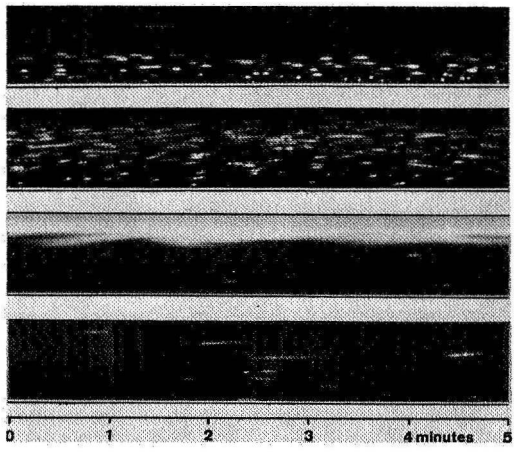


FIGURE 3. Z-scan film records of the passage of birds in heavy migration (A, B) and in low density migration (C, D). Film movement was 1/2 mm per sec. Height of film strip corresponds to range of 4 km: A, C with vertical beam; C with rain clouds above 2500 m; B, D with low elevation.

tensity modulation) and recorded on continuously moving 36 mm film (fig. 3). The width of the film corresponds to the surveyed range of 4 km; the longitudinal axis shows the time of passage for each target.

In the case of the low-elevation beam, attention must be paid to the fact that the number of echoes appearing within the surveyed range intervals depends on the flight directions of the birds. To diminish this influence, the number of echoes was divided by the cosine of the angle α between the supposed principal direction and the mean of the actually measured tracks (fig. 2). After having eliminated the echoes of insects and bats (ref. 2),[1] the frequency of migration Q (i.e., number of bird transits through a cylinder of 100 m in height and 100 m in diameter during 1 hour) was calculated by dividing the number of bird echoes in a certain height interval by the corresponding area of the performance diagram of the beam.[2] If the spread of the flight directions is low, this frequency corresponds to the rate of passage of birds through a vertical area of 100 × 100 m normal to the mean direction of migration per hour. The density of migration D (number of birds in an air volume with a base of 2 km² and a height of 250 m) was calculated by dividing frequency Q by mean groundspeed of bird targets in the height interval considered and multiplication by factor 50.

Because the size of the surveyed space is very small and provides only the local flight frequencies, all samples taken during a night (normally between 2100 and 0300 hours) were summed. This is considered a useful estimate of the flight activity in northeast Switzerland.

GROUPING OF NOCTURNAL MIGRANTS

The analysis of echo signatures shows whether there are 1, 1 or 2, 2 or 3, or more birds in the pulse volume considered (see fig. 4). This permits us to establish the number of birds that fly in one pulse volume at various times of day. The pulse volume at medium ranges may be thought of as a cube with side lengths of 100 m. Figure 5 shows that in spring migration we have recorded almost exclusively single birds during the night, while flocks prevailed in the daytime.

The possible existence of some sort of loose groups during night migration was examined by measuring the distances between neighboring echoes on the films from the Z-scan display.[3] The frequency of the various

[1] Also, BRUDERER, B.: Radarbeobachtungen über den Frühlingszug im Schweizerischen Mittelland (to be published).

[2] Because small passerines make up the biggest part of the migrating birds (~ 82 percent), we took $\sigma = 8$ cm² as the standard radar cross section to calculate the performance diagram.

[3] BRUDERER, B.: Radarbeobachtungen über den Frühlingszug im Schweizerischen Mittelland (to be published).

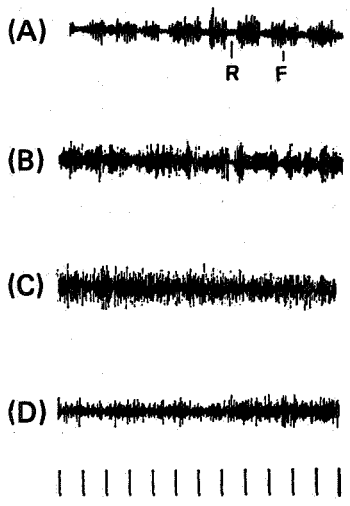


FIGURE 4. Four echo signatures showing difference between single birds and flocks of different size. To eliminate strong slow signal fluctuations, low frequencies were reduced by a high-pass filter, while wing-beat frequencies (above ~ 6 Hz) pass optimally. Vertical lines at bottom mark intervals of 1 sec. (A) Wing-beat pattern of a single starling (*Sturnus vulgaris*) with typical change of flapping (*F*) and resting (*R*) periods; (B) Signal of two sky larks (*Alauda arvensis*) with interfering beating and quiescent phases of the two birds; (C) Echo signature of six starlings, with continuous fluctuations; (D) Signature of 12 starlings with continuous fluctuations of less amplitude.

distances was plotted in histograms (fig. 6). These diagrams show that minimum distances between birds are about 50 m and that distances of 150 to 300 m are most frequent. This peak of the distribution persists even when the density of migration decreases; this means that, on nights with light migration, only some of the distances between birds grow larger, while a noticeable fraction remains constant. This fraction may be interpreted as a hint of the existence of loose bird groups in addition to a large number of individuals flying alone. We estimate that the number of individuals within such a formation in low density migration is 2 to 25, most frequently 2 to 10; with high density of migration the number of birds per flock may increase (refs. 3 and 4).

PROBLEMS OF FLIGHT VELOCITY

Bellrose (ref. 5) pointed out that groundspeeds are not influenced in an additive way by the following component of the wind. Our own measurements have, in a general sense, confirmed this statement. Yet our results show—with much better correlation—an alteration of groundspeed by ⅔ of the component of the wind vector along the birds' track direction, while in Illinois Bellrose found an increase of only ⅓ of the (favorable) wind component. As an example (fig. 7) we give the optimally correlated data from 64 chaffinches (*Fringilla coelebs*). If the difference between track and heading is low (sidewind component negligible), as in these cases, the decrease of airspeed is about ⅓ of the corresponding wind component. Our results indicate that birds must recognize accurately the speed and direction of the wind and that they seem to know and to actively choose an appropriate airspeed under different wind conditions.

Another striking phenomenon is the increase of the average airspeed with height. It is, according to our measurements, 2 to 3 km/hr per 500 m of height or about 10 percent per km (see fig. 8). The theoretical rise in speed due to the decreasing density of the air is only about 5 percent per km of height. This leads us to the conclusion that fast-flying birds (ducks, waders) prefer higher flight levels than most of the small passerines with low speed capabilities.

IDENTIFICATION OF BIRD ECHOES

The recorded signals of the AGC allow determination of wing-beat frequency as

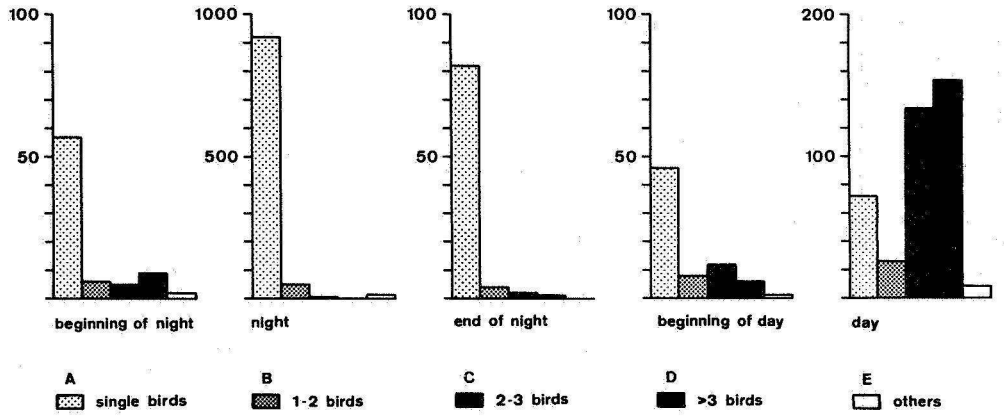


FIGURE 5. Distribution of echo signatures of single birds and flocks in day and night migration (classes A to D). Class E (others) includes signatures of bats and insects (main mass of insects being eliminated already in advance by a sensitivity time control, STC). The beginning of the night (sunset until 1 hr after sunset) contains some groups which are mostly caused by roosting starlings (*Sturnus vulgaris*) and black-headed gulls (*Larus ridibundus*). Night migration (1 hr after sunset to 1 hr before sunrise) comprises scarcely any flocks. End-of-night migration (1 hr before sunrise until 1/2 hr before sunrise) shows a similar composition as night migration. Beginning-of-day migration (1/2 hr before sunrise until sunrise) shows that formation of flocks begins fairly late. In daytime migration (after sunrise) the flocks prevail. (Autumn migration shows even fewer single birds.)

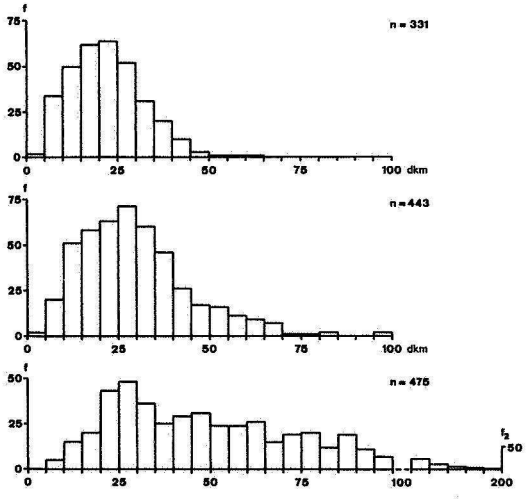


FIGURE 6. Distribution of distances between birds in night migration; the abscissa giving the measured distances in dekameters (1 dkm = 10 m) the height of the columns (ordinate) representing the frequency of each distance. Upper diagram for heaviest migration, middle diagram for medium to high frequency of migration, and lowest diagram for light migration. The fact that in light migration a considerable fraction of distances between birds remains in the same size category as in heavy migration may be interpreted as a hint of formations with spaces between individual birds of 100 to 300 m, independent of migration volume.

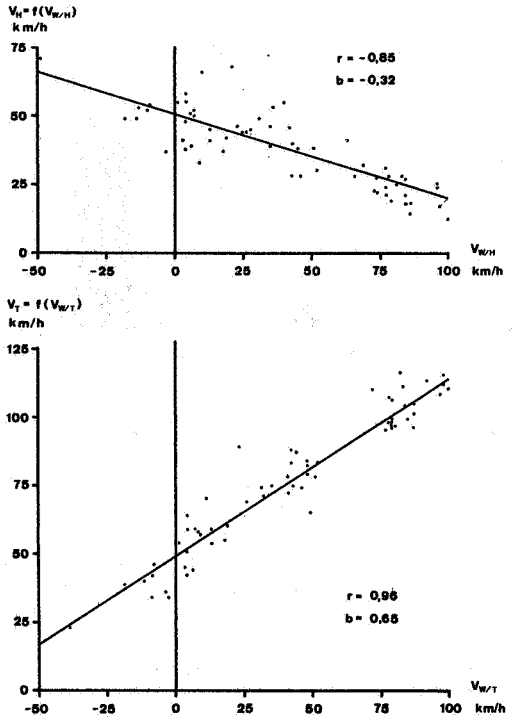


FIGURE 7. Wind influence on flight speeds of chaffinches (*Fringilla coelebs*). Top diagram shows correlation between calculated airspeed (V_H) and wind vector in the direction of heading ($V_{W/H}$). r is correlation coefficient; b is regression coefficient (slope of regression line). Lower diagram shows correlations between groundspeed (V_T) and wind component in the direction of track ($V_{W/T}$). Night migration showed correlations similar to this example of day migration.

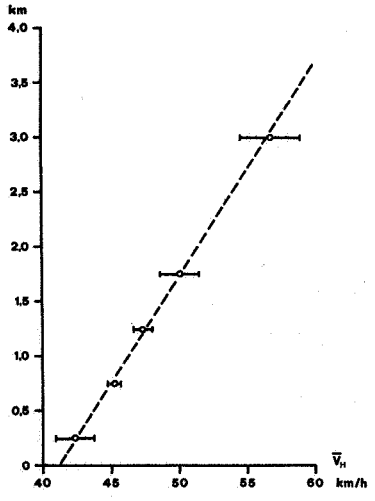


FIGURE 8. Increase of average airspeed ($\bar{V}_H$) with height. Circles mark the mean of the airspeeds for five intervals of height (four comprising 500 m each and one summing up heights between 2000 and 4000 m). Horizontal lines show the standard error ($s/\sqrt{N}$). Differences between the five means are—in spite of the large spread of the single dates —statistically significant on levels of $p = 0.07$ to 0.01.

well as the duration of flapping and quiescent periods within the wing-beat patterns of a bird (see fig. 9). Additional information of less diagnostic value may be obtained by calculating the typical flight velocity of a particular species (airspeed plus $\sim 1/3$ of the wind component in the direction of heading)[4] and by measuring its radar cross section (ref. 6).

In daytime migration the species belonging to a certain echo signature can be identified with the help of a telescope mounted parallel to the optical axis of the antenna. For night migration we need much more film material showing flight of night migrants in daytimes; this is needed to establish a correlation between taxonomic classification and the "radar" or "echo" species determined from echo signatures (ref. 7). In order to make the sampled echo signatures available for immediate use we have established a provisional radar classification without attempting a zoological one (fig. 10). An example of the application of this radar classification is given in part II.

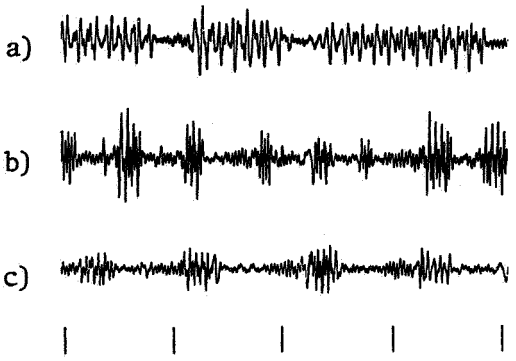


FIGURE 9. Echo signatures of visually identified day migrants: (A) Mistle thrush (*Turdus viscivorus*); (B) Chaffinch (*Fringilla coelebs*); (C) White wagtail (*Motacilla alba*). The three species can be distinguished by wing-beat frequency and by length of flapping and quiescent periods within their flight; vertical lines at the bottom mark intervals of 1 sec. Echo signatures of night migrants may be classified according to the same parameters (fig. 10), but to date we have not established a correlation with ornithological classification.

VOLUME AND HEIGHT OF SPRING MIGRATION UNDER DIFFERENT WEATHER CONDITIONS

In all graphs of figures 11 to 14 the length of the horizontal columns indicates the frequency (Q) of migration; the position of the circles marks the corresponding density (D) of migration (an average groundspeed of 50 km/hr leading to the same values in both frequency and density).

Figure 11 shows the average altitude distribution of spring migration derived from two periods of 3 weeks (1968 and 1969). The distribution agrees fairly well with the results published by Eastwood and Rider (ref. 8). Altitude distribution as well as the intensity of migration vary on a large scale according to weather development. In figure 12, 40 nights of observation were divided into nine typical weather situations. They show volume and height of migration during a weather development comprising five situations with anticyclonic character (1 to 5) and four situations in which cyclonic influences prevail (6 to 9):

(1) East side of a high pressure area (with cold northerly winds)

(2) Central part of a meteorological high (with light and variable winds)

(3) Flat pressure areas with anticyclonic character (winds light, in the cases considered, mostly from W to SW)

(4) Southern part of a high (NE to E winds, partly with Foehn winds in the Alps)

[4] The sign $\sim$ is necessary because the value of $1/3$ is somewhat too high in cases with large components of wind normal to the heading.

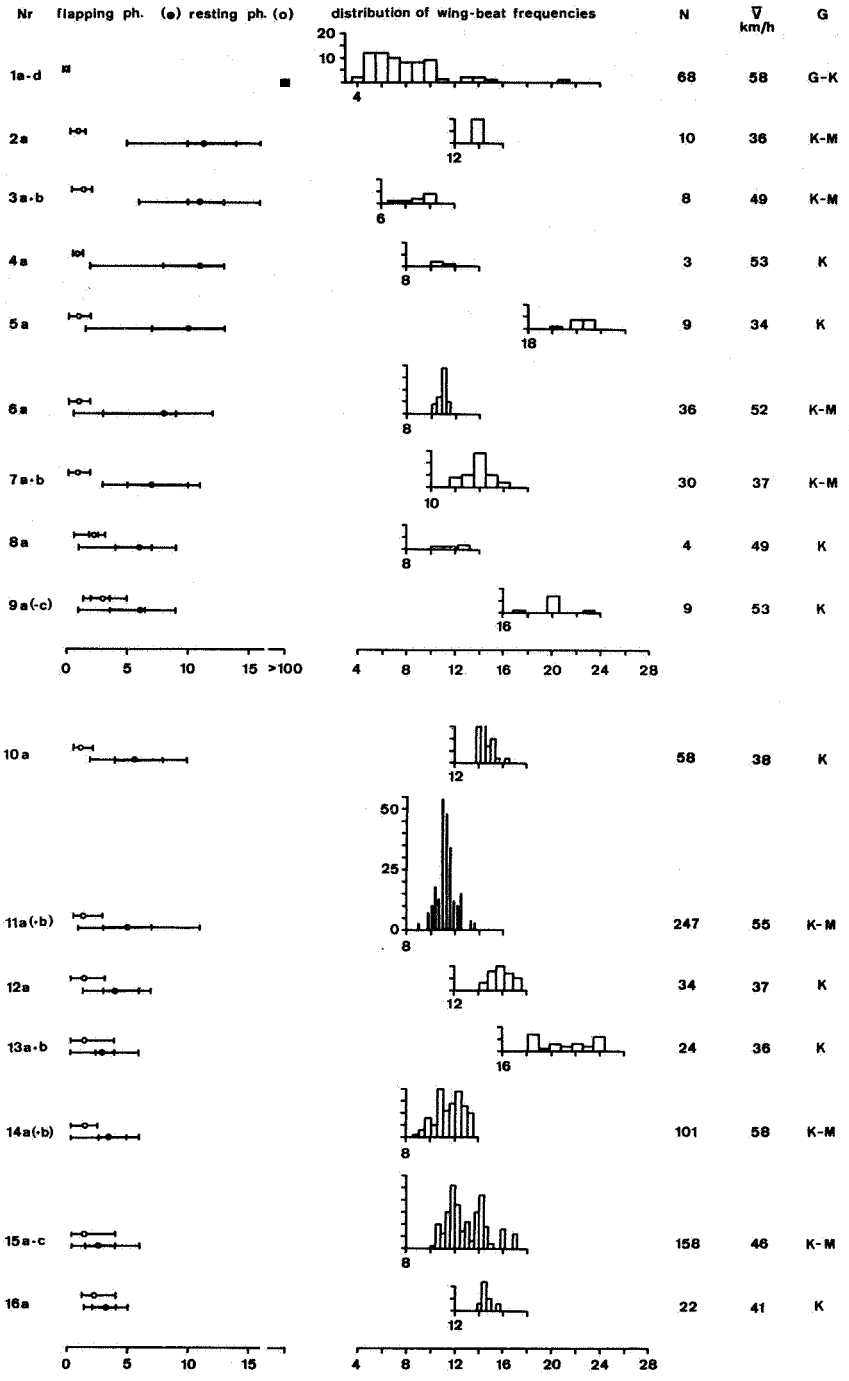
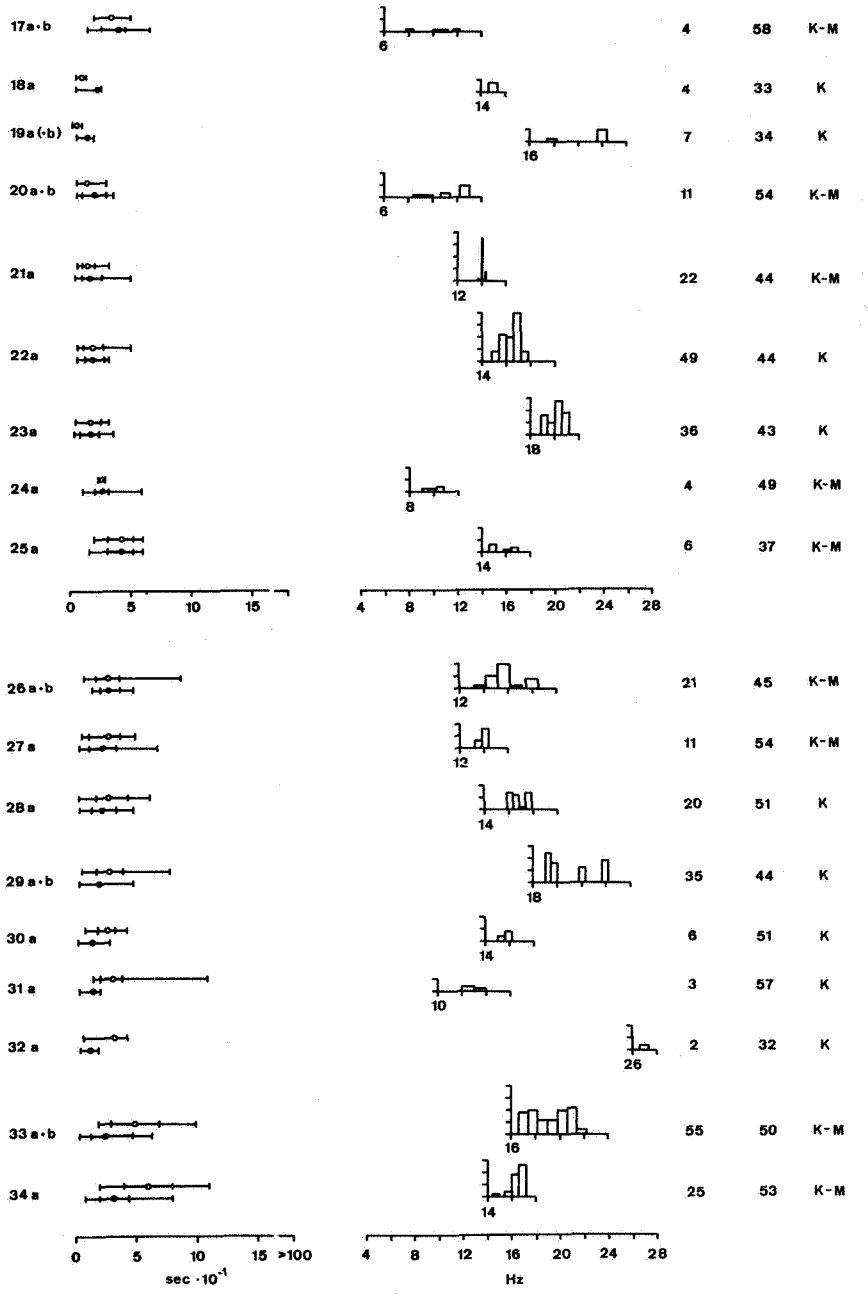


FIGURE 10. Provisional classification of "echo types" and "echo species" recorded during April 1969. A first arrangement according to the length of flapping periods (●) and quiescent



phases (O) and their spreads (—) leads to 34 echo types, each of which may be divided into one, two, or more (*a*, *a* + *b*, or *a* — *z*) echo species with the help of wing-beat frequencies. *N* marks the number of individuals in every type; *V* is mean of calculated velocities of species ($V_H + \sim 1/3\ (V_{W\,H})$; *G* may give a hint to the size of the birds contained in one type (*G* = large; *M* = medium; and *K* = small).

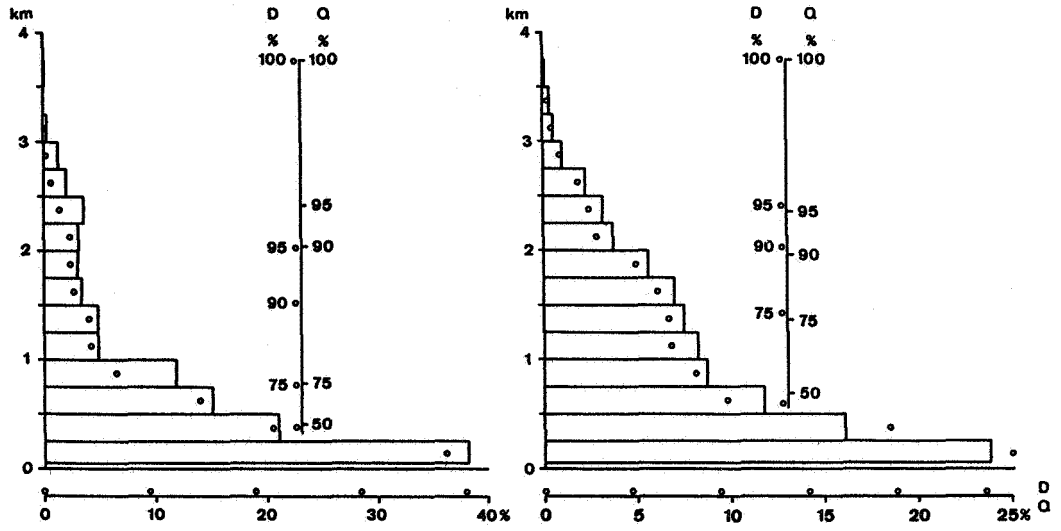


FIGURE 11. Average altitude distribution of spring migration. On the abscissa the percentage of frequency (columns) and density (circles) of migration is indicated for height intervals of 250 m. At the left—day migration; at the right—night migration.

(5) W to SW side of an anticyclone (E to SE winds, often Foehn winds in the Alps)

(6) Approaching warm front (all cases after the passage of a previous low pressure area)

(7) Warm sector (could be interpreted in some cases also as the NW edge of a warm high pressure cell; SW winds)

(8) Central regions and disturbance zones of low pressure areas (wind variable in direction, often strong)

(9) Rear side of low pressure areas (in the present cases mostly with winds from sector north to west). This situation leads back to situation 1.

In the cases we could examine, heaviest migration occurred in the warm sectors of cyclones (not too near the frontal systems) and on the W to SW side of anticyclones. Lightest migration was observed in zones of precipitation (center of low and fronts) and on the rear side of the low pressure areas, as well as on the east side of the high pressure areas.

With respect to the question whether the level of migration might be higher with tail winds than with head winds, we believe that the reality is much more complex than the question. Perhaps the question should be restricted to anticyclonic conditions, because we have noticed several cases with low migration in the neighborhood of frontal systems in spite of tail winds (fig. 13). On the other hand topographic features may induce wind distributions differing from the normal case (i.e., windspeeds increasing with height), so that anticyclonic situations with opposed winds may give rise to quite a similar distribution of migrating birds as situations with tail winds, whenever windspeeds are favorable at the same levels (see fig. 14). Furthermore the facts may often be blurred by differences in behavior of different species or even by alterations of flight levels by the same species during one night (see part II).

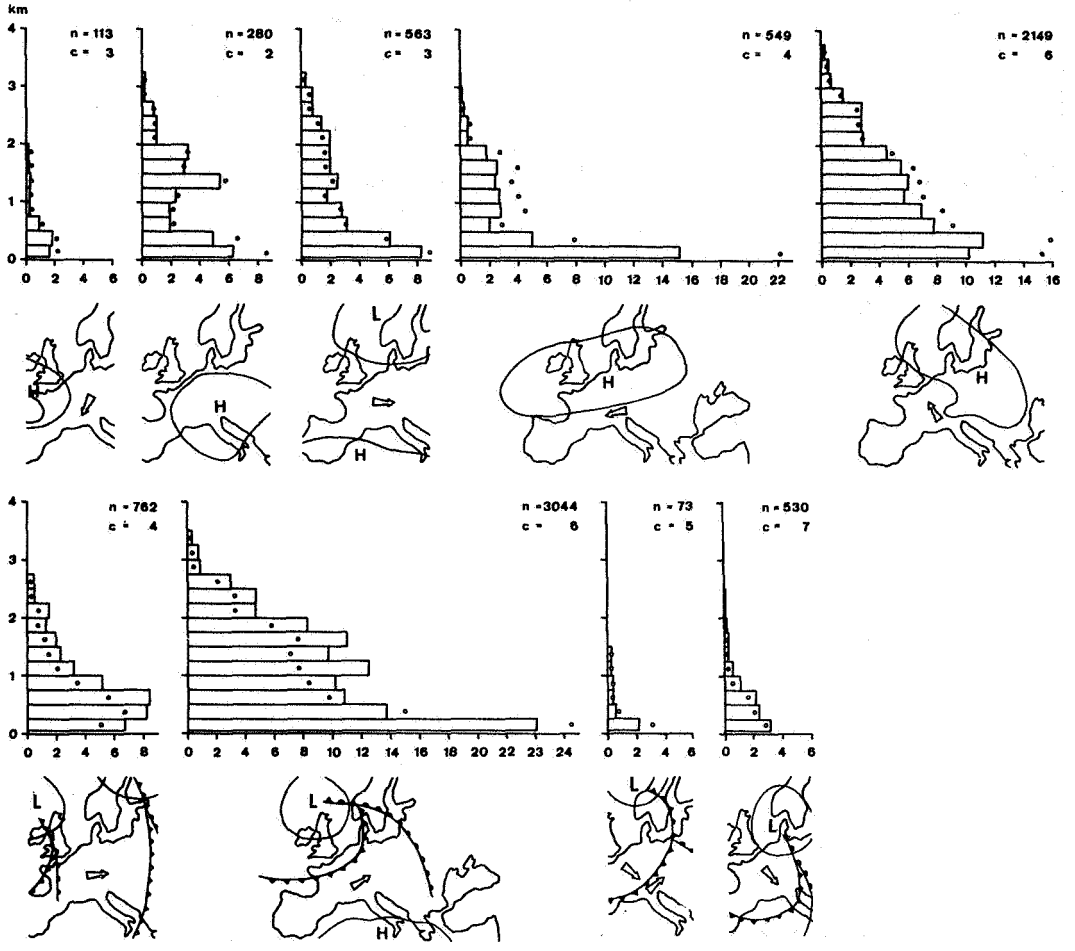


FIGURE 12. Intensity and height of migration derived from 40 nights of observation with respect to nine different weather situations. Number of nights within each situation is indicated as *c*, the number of the counted echoes as *n*. Below each migration diagram, a sketch indicates the appropriate weather situation with the prevailing wind direction. Altitude distribution (ordinate) is given for height intervals of 250 m. The abscissa gives frequency (columns) and density (circles) of migration as defined in the text.

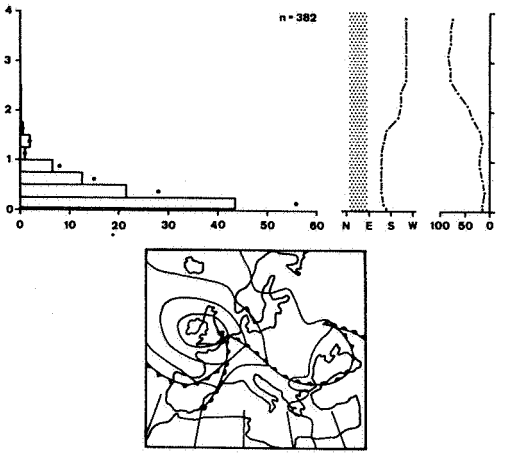


FIGURE 13. Low level of migration in the neighborhood of a frontal system (April 21 and 22, 1969) in spite of tail winds. Diagram on the right shows windspeeds in km/h. Middle diagram indicates direction from which wind is blowing and main sector toward which birds are migrating (dotted area). The weather situation at midnight is shown below. Diagram on the left corresponds to those in figure 12.

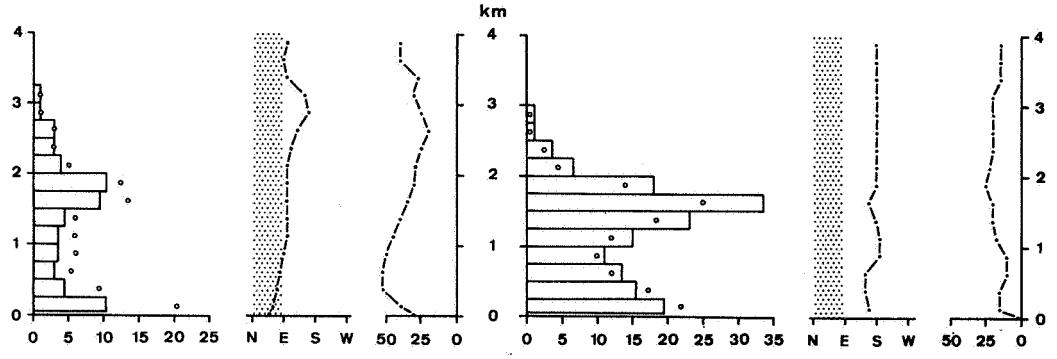


FIGURE 14. Altitude distribution of migration and wind conditions in nights of March 23 and 24, 1968 (with a strong tail wind component) and in nights of April 5 and 6, 1969 (with a head wind component); same mode of diagrams as in figure 13. In the case of tail wind, the height with lightest wind shows lightest migration; in the case of head wind, lightest migration occurred at levels with highest windspeeds.

Part II by P. Steidinger

DEPENDENCE OF MIGRATION FLIGHT DIRECTIONS UPON WIND DIRECTIONS

Taking as an example one of the most interesting nights in our radar observation period in the spring of 1969, we will show one of the potentialities of our tracking radar in orientation research.

Ceiling balloons with a metallic reflector, tracked with our radar up to a height of 4000 m above ground informed us about wind directions and windspeeds at all altitudes we needed. At intervals of 30 seconds we photographed the measuring instruments of the radar which showed us the positions of the balloon. From the different positions we computed wind directions and windspeeds. Figure 15 shows graphs of the three wind measurements we carried out on the night of April 19 and morning of April 20. Note that at lower levels the wind blew from SE or S and higher up from SW.

We tracked the birds with our radar in the same manner as the balloons. We normally observed each bird during 2 minutes and took five pictures of the measuring instruments at intervals of 30 seconds. From these five positions we computed height, track direction, and track speed. The possibility of computing the exact altitude of migration with the information from the tracking radar is an important advantage when compared to our investigation with the surveillance radar of Zurich Airport (refs. 1, 9, 10, and 11).

Figure 16 shows the height and the tracks of the birds observed between 2010 and 2340 hours on April 19. We computed heading and airspeed based on the wind measurements closest to a bird observation (fig. 17). Note that tracks and headings of high flying birds in this first part of the night show quite a similar distribution to those of low flying birds.

Figures 18 and 19 demonstrate tracks and headings between 0130 hours and 0530 hours. The high flying birds observed in this second part of the night show distributions of tracks and headings similar to those of birds observed in the first part of the night (compare fig. 18 with fig. 16 and fig. 19 with fig. 17).

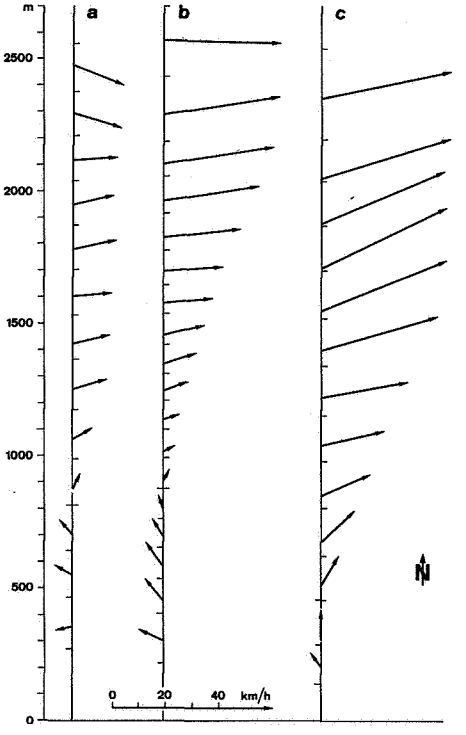


FIGURE 15. Wind measurements: (A) April 19, 1969, 1751 to 1813; (B) April 20, 1969, 0053 to 0109; (C) April 20, 1969, 0809 to 0821. Ordinate: meters above ground. Direction of arrows shows wind direction in the corresponding height. Length of arrows indicates windspeeds in km/h (compare with windspeed scale).

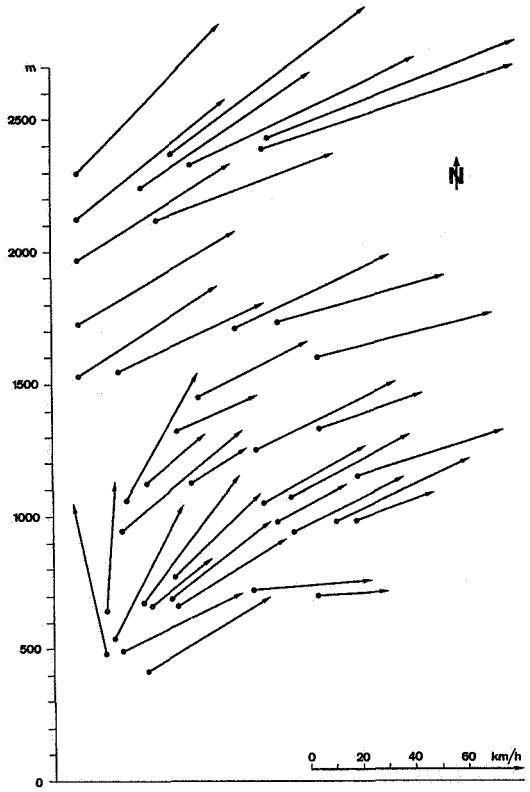


FIGURE 16. Tracks of birds observed between 2010 and 2340 on April 20, 1969. Ordinate: meters above ground. Each point at the end of an arrow shows migration height of individual bird. Direction and length of arrow indicate track direction and track speed.

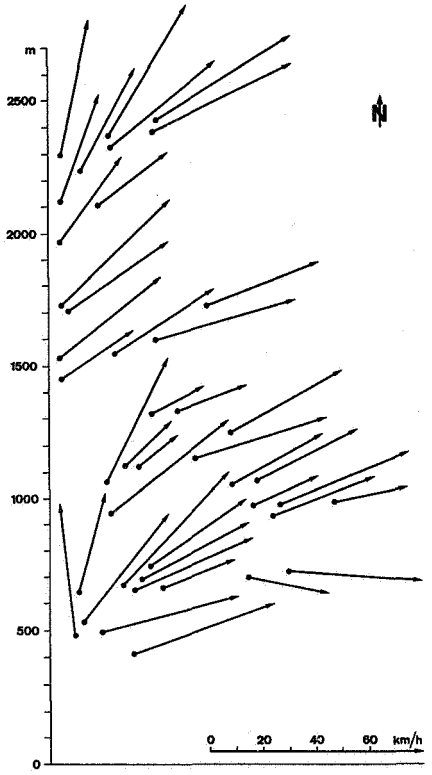


FIGURE 17. Headings of birds observed between 2010 and 2340 on April 19, 1969. Ordinate: meters above ground. Each point at the end of an arrow shows migration height of individual bird. Direction and length of arrow indicate heading direction and airspeed.

Tracks and headings of the low flying birds in this second part of the night point mainly to the north. The distribution of tracks and headings below 850 m above ground is statistically different at the 0.001 level from the distribution of tracks and headings above 850 m (Wilcoxon test). These northerly flight directions occurred more often during the second part of this night than at any other time during our observations.

Comparing tracks and headings of low flying and high flying birds (figs. 18 and 19) with the appropriate wind directions during the night (fig. 15), we see that the birds, at least in this case, migrate at such a height that they have favorable winds. Birds migraing to the north fly lower than those migrating to the northeast. This finding is in good agreement with Bellrose (ref. 1), who reported, on the basis of his radar observation in the midwestern United States: "Our radar findings demonstrate that birds have a phenomenal understanding of winds. They select nights and altitudes having favorable directional winds and favorable windspeeds."

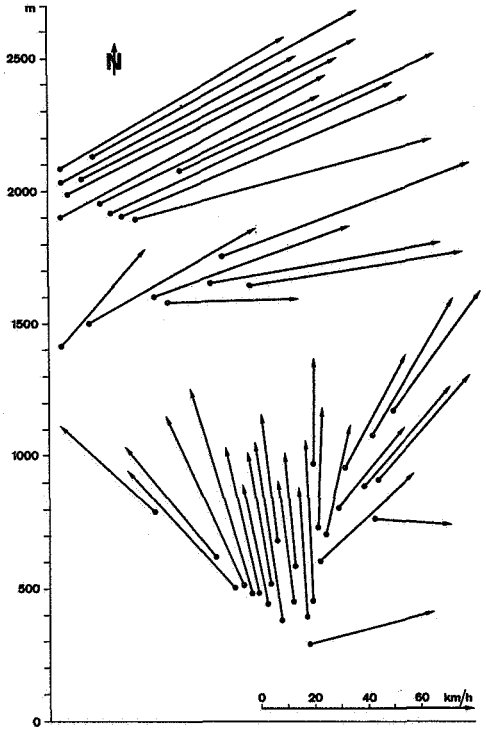


FIGURE 18. Tracks of birds observed between 0127 and 0526 on April 20, 1969. For explanation see figure 16.

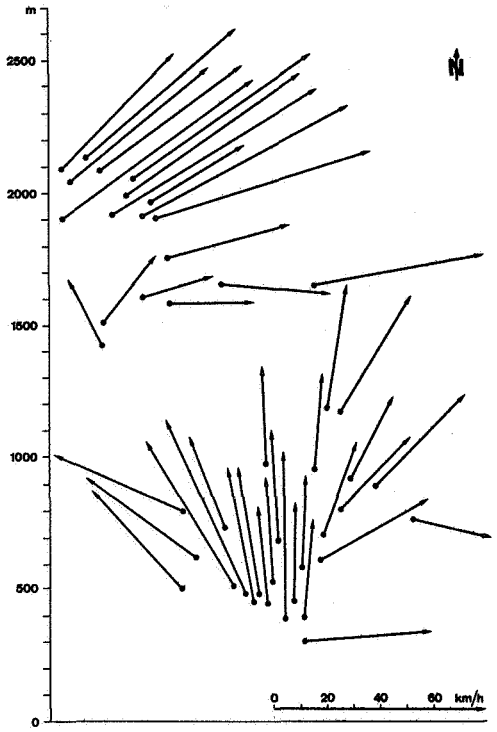


FIGURE 19. Headings of birds observed between 0127 and 0526 on April 20, 1969. For explanation see figure 17.

Our analysis of echo signatures (refs. 2 and 6) indicates that species traveling at different heights during the first part of the night change altitudes to fly at one particular height in the second part. It is possible that migration calls could help the birds to find a height with favorable winds. For example, a bird may hear the calls of another bird of the same species flying at a higher altitude. If the wind higher up is more favorable, the higher flying bird will move ahead faster. Realizing this, the lower bird might climb up and thus will find a height with more favorable winds.

The observation that in the first part of the night there were only few birds with a northerly track raises another question: Where and when did all the low flying birds that were seen migrating to the north in the second part of the night take off? We see two possibilities:

(1) They started late at night, north of the Alps.

(2) They took off early at night, south of the Alps.

But we may ask: After crossing the mountains at a height of about 2500 m above sea level, do night migrants lose so much height that after a further flight of 150 kilometers they are only at about 1000 m above sea level? Perhaps they do, especially if the winds near the ground are more favorable than higher up. We are not able to answer all the questions raised in this paper. But we hope to have shown some possibilities of using a

tracking radar in migration research. For this purpose we have discussed a few specific problems, some of which we will try to solve in the near future.

SUMMARY

1. With the help of an X-band (3 cm) tracking radar, data on spring migration in northern Switzerland were collected during two periods of 3 weeks in 1968 and 1969.

2. A vertical beam method, improved by counts with low elevation of the beam, allowed quantitative recording of the frequency of migration at all heights between about 30 and 4000 m above ground. Density of migration was calculated with the help of the measured speed of migration.

3. The qualitative analysis of migration was based on automatic tracking of single targets and comprised: (a) measurements of groundspeed, height and track, (b) recording of echo signatures based on AGC signals, (c) measurements of local upper winds with radar-tracked balloons, (d) calculation of airspeed and heading with the help of the measured wind data.

4. In night migration loose groups of birds seem to exist in addition to large numbers of individuals flying alone, the distances between grouped birds being in the order of 100 to 300 m. The airspeed of night migrants increases with height. Airspeed decreases in tail winds and increases in head winds.

5. Heaviest migration was observed in warm sectors and on the W to SW side of high pressure areas.

6. The question of the relationship between height of flight and wind direction is a very complex one, and must be considered at least in relation to the prevailing weather situations and the local topography.

7. In the second part of the paper we discuss the dependence of track and heading directions upon wind directions on a night with particularly interesting winds. Our finding is that birds migrated most frequently at heights of favorable winds.

ACKNOWLEDGMENT

We are very greatful to the firm Contraves AG and to the Swiss Army for making available to us the radar equipment and for the active assistance they gave us during our work. Financial support by the Dr. Fritz Hoffmann—La Roche Foundation is gratefully acknowledged, as well as the kind support and encouragement of our study by A. Portmann and G. Wagner. We wish to thank the Meteorological Office of Zurich Airport for supplying weather data and to A. Urfer for summarizing these data in daily reports. All further cooperation and help which made possible our research is heartily acknowledged.

DISCUSSION

QUESTION: What is the range of flock size in the passerines? Do the nocturnal migrants break up in flocks at the beginning of darkness?

BRUDERER: In spring the flocks number from 2 to 20, normally from 3 to 10. In autumn migration they are in the order of 5 to 30 or even larger.

The flocks occasionally observed visually at the beginning of darkness were mostly those of roosting starlings and black-headed gulls; thus, we are not able to say if there are any night migrants breaking up into flocks. We know only that starlings migrate closely flocked in the daytime and that we have no echo signatures of flocks recorded during the night. Yet we know from captures in the alps that starlings do migrate during the night, and we have several echo signatures of night migrants which are similar to those of singly flying starlings.

MADISON: How do you distinguish between migrant and nonmigrant starlings?

BRUDERER: Nonmigrants normally do not fly at night. At twilight, roosting starlings can be recognized because we know the direction of their roosts which are not the same as the direction of migration. Furthermore, the roosting birds flew relatively low at our observation point. In the daytime only, the direction of migration and the constancy of the flight tracks can give some indications for distinction.

GWINNER: You have presented data indicating that the groundspeed is kept constant if the birds are exposed to back winds. To what extent does it remain constant?

BRUDERER: The groundspeed doesn't remain constant; it was only said that it was not influenced in an additive way by the wind vector along the birds' track. In our measurements about two-thirds of the wind component in question were added to the groundspeed of the birds, so that in a tail wind the birds seem to lower and in a head wind to increase their own effort. A possible mathematical explanation to these observations is given by Pennycuick (ref. 12).

EVANS: Your analysis suggests that the groundspeed of a bird is not the vector sum of the wind with a constant airspeed. Could this result be explained by differences in airspeed according to the weight of the bird? According to Pennycuick's calculations, one would expect a bird of a certain weight to maintain a certain airspeed to achieve maximum range. As that bird gets lighter during a long flight, so its airspeed should decrease.

BRUDERER: To answer your question it would be necessary to measure the weight of a bird with high accuracy so as to recognize the decrease of the bird's weight according to the utilization of fat. With our methods we were only able to say to which of three size categories a bird belongs. Perhaps with better methods it will be possible to show if the average weight of a species during a night decreases until sunrise. If it would be so (and it should), you are right in thinking that the airspeed of a species should slow down if the birds don't raise their flight level. However, the speed changes shown in this paper can't be explained in terms of weight changes because we excluded this problem by treating all the data of one night or even the data of several nights (or days) as a whole; speed differences arising from weight changes during a night are so eliminated statistically.

WILLIAMS: Perhaps it would be interesting to add another point of view to this problem with an example of a track of a single bird target descending through a wind sheer having a variety of winds. We were able to show that it makes considerable difference what a bird can see. If the birds can see and it is clear, they compensate both for direction and the speed of the wind. In other words, the airspeed and the heading of the birds both change. If they can see either the stars or the Earth, neither the airspeed nor the heading of the birds change even though they descend through considerable wind sheer. They do not compensate for either.

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Nocturnal Bird Migration in Opaque Clouds

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The Rockefeller University
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IT IS GENERALLY RECOGNIZED that birds can maintain directional orientation by means of the Sun or stars (ref. 1). But recent radar observations have demonstrated that much migration occurs under overcast skies (ref. 2). Therefore, it is of primary importance for theories of bird navigation to inquire whether birds that migrate on cloudy nights fly above, below, within, or between layers of cloud, and whether the clouds are thick enough to conceal the sky, the ground, or both. If birds do fly within or between cloud layers, how long do they remain cut off from sight of sky or ground, and how does their orientation compare with that displayed on clear nights? Evidence for migratory orientation within cloud layers has been presented by Bellrose and Graber (ref. 3), although flight directions of birds that appeared to be in clouds were distinctly more variable than on clear nights. The radar used in these studies recorded only intermittent positions during short segments of any one flight path, so that straightness and levelness of flight could be estimated only very roughly. Eastwood and Rider (ref. 4) also reported instances in which migrating birds were flying at night within a thick layer of clouds, but they do not report any flight directions under these conditions nor whether the birds were flying level, climbing, or descending.

In hopes of clarifying the degree to which migrants maintain oriented flight in or between clouds, I have employed a tracking radar to measure as accurately as possible the flight paths of migrating birds on nights with opaque stratus clouds at low altitudes. Many colleagues provided indispensable collaboration in essential phases of this work. On three nights during the spring of 1970 when fog and low stratus clouds were present continuously over a broad area, we observed numerous birds flying in appropriate directions for distances up to 3 or 4 km. A special effort was made to analyze all available meteorological data concerning the vertical and horizontal extent of the cloud layers. Local wind velocities were measured when feasible by tracking a balloon with the same radar as it rose through the range of altitudes where birds were observed. The combined evidence strongly supports the conclusion of Bellrose and Graber that birds sometimes migrate in appropriate directions inside opaque clouds.

METHODS

The Radar

The most suitable radar we were able to obtain was a military surplus 3 cm (X band) type AN/GPG–1 unit, otherwise known as a

T–9 tracker from the "Skysweeper" antiaircraft system. It is basically similar to the radar used by Gehring and Bruderer and Joss (refs. 5 and 6). A tracking radar contains the important feature that electronic circuits automatically keep the beam aimed at a given target once the radar is "locked on" to it. Thus the whole track can be measured quite accurately as long as the autotracking circuits are locked on to a given bird or flock.

Radars such as these do not yield pronounced echoes from clouds consisting of small water droplets, although clouds with large droplets or active precipitation are clearly revealed (ref. 7). Hence our radar could track birds through several hundred meters of stratus cloud. We mounted this instrument on a trailer, so that it could be moved to any location accessible to automobiles. Power was supplied from a gasoline-engine driven generator when line power was not available. The nominal peak power output of this radar was 40 kilowatts; its pulse width was 0.25 μsec; and the pulse repetition rate was approximately 3800/sec. The antenna was only 75 cm in diameter which yielded a nominal beam width of 3°, but the autotracking circuits were designed to track with an accuracy of approximately $\pm$ 0.03°, and in practice this degree of accuracy was apparently achieved. The range dial could be read to within $\pm$ 3 m, so that in theory a bird at 1000 m slant range (range along the radar beam) could be located within a very few meters. Since ground clutter made it very difficult to calibrate the radar with fixed targets at known positions, the best evidence of the accuracy was obtained from the straightness of the straightest tracks recorded. Instrumental errors or random inaccuracies would be most unlikely to convert an irregular flight path into an apparently straight one. A typical example from the longest and straightest tracks (2134, April 30, 1970) covered a total distance of 3400 m in 144 sec. During this period of tracking the azimuth values shifted gradually from 204° to 055° (North = 000°); the elevation rose from 33° to 68° and then fell to 25° as the bird passed nearly overhead; while the slant range decreased from 1968 to 1144 m and increased again to 2248 m. The altitude of the bird varied between 1025 and 1065 m. Throughout this track all positions recorded by the methods described below fell within 40 m horizontally and vertically of a straight line. The departures from such a line were not random, as can be observed in several of the figures discussed below, so that it seems likely that we were continuously measuring the positions of many birds with an accuracy of $\pm$ 5 or 10 m.

In the actual operation of this tracking radar, bird echoes could be observed either on a small (7.5 cm diameter) PPI screen or on an A-scope display as the azimuth and elevation controls were operated manually to scan the sky. When appropriate manipulation of the controls caused the radar to lock-on to a bird or other target, the bird's elevation, azimuth, and range could be read from dials. But it was impossible to take full advantage of the information provided by the radar without recording the position of each bird as accurately and continuously as feasible. Slight modifications were therefore made to generate dc voltages proportional to azimuth, elevation, and range. These dc voltages in turn were converted into frequencies from approximately 600 to 6000 Hz that could conveniently be recorded on three channels of a four-channel tape recorder (Precision Instruments model 6100). The fourth channel was used to record voice notes or other signals. Each frequency could be reconverted with the aid of calibration data into azimuth, elevation, and slant range, by use of an electronic counter or frequency meter. The resulting values could then be converted by

simple trigometric calculations into the bird's position. But an accurate and continuous record clearly called for computer data reduction. The tape-recorded analog frequency data were read into a Linc 8 computer which used 1-sec sampling intervals to count the number of cycles per second. An output tape was then prepared with a digital number tabulation for each second of the azimuth, elevation, and range frequencies as played back from the tape recorder. This tape was then utilized in conjunction with a Fortran program prepared by D. K. Riker for processing by the CDC 160G computer at The Rockefeller University Computer Center.

The final output from the computer consisted of a print-out and a graphic plot. The former provided once per second the following quantities in numerical form:

(1) The three original frequencies as played back from the tape recorder

(2) The corresponding values of azimuth, elevation, and slant range

(3) The X, Y, and Z coordinates of the bird (X = East-West, Y = North-South, Z= altitude relative to the radar)

(4) The horizontal and vertical distance that the bird had moved between each successive pair of readings

The graphic plot displayed the bird's XY position and separately its altitude as a function of distance traveled over the ground. The XY graphic plots were superimposed on topographic maps photographically enlarged to the same scale, to display any correlations between flight path and topography.

It was not possible to maintain continuous tracking of all bird targets that could be observed on the PPI or A-scopes. Consequently only cases where such tracking was maintained for at least 30 seconds without evident discontinuities are considered below (except as noted for a few tracks on May 16–17, 1970). This means that we gathered significant data only from reasonably steady targets. Since the tracking circuits were designed to keep the radar aimed at the strongest target falling within its beam, it would sometimes shift from one bird or flock to another. Such cases were excluded from consideration unless each portion of the track, considered separately, was of adequate length to be of interest.

The longest bird tracks we were able to record continuously were about 5 km. The lowest elevation at which birds could be reliably tracked despite radar echoes from the ground was ordinarily about 10°, although at one location on a ridge, tracking did prove possible down to elevations of 0°, which represented a clear view out into adjacent valleys. The maximum range at which most bird targets could be maintained in the autotracking mode of the radar varied between 2000 and 2500 m. Many birds were lost at shorter ranges for unknown reasons, and an occasional bird target, presumably a very large bird or a dense flock, could be tracked to 3500 m or more. The data presented in this paper are not at all a random sample of birds migrating over the location of our radar. For example, we did not make sustained efforts to search for birds at the highest possible altitudes, since we were primarily interested in obtaining tracks as long as possible, but some birds were tracked as high as 2000 m above the radar. In spring we usually searched for birds with the radar beam pointed roughly south or southwest and at elevations between 20° and 35°, because this facilitated the recording of long tracks as birds approached, passed nearly overhead, and receded to the north or northeast. For tracking we selected primarily birds that were picked up at nearly maximum range and high enough to avoid ground echoes. On the other hand there were often times when no birds could be detected by this procedure, and we then searched in

other directions and at other elevations of the beam. Our procedure tended to exclude birds flying both at the lowest and the highest altitudes. Hence the tracks described here tended to be those of birds or flocks passing fairly close over our radar in the customary direction of spring migration.

Artificial targets, approximate spheres formed from aluminum foil suspended about 0.5 m below meteorological pilot balloons, could also be followed to about the same distances. These metal targets ranged in diameter from about 10 to 30 cm, and one might at first suppose that they would be detectable at much greater distances than birds. But as discussed by Eastwood (ref. 8) and Bruderer and Joss (ref. 6), water reflects 3 cm microwaves more than half as strongly as a metal sphere of the same size. Since the range at which a given radar system can detect a target varies as the fourth root of the target strength, this difference becomes trivial in comparison to the other variables involved in tracking birds by radar. Likewise variations in ground return and fluctuations in echo amplitude from both birds and metallic targets allowed only rough comparison of tracking ranges. But it does seem clear that our artificial targets were tracked to approximately the same distances as birds.

On several occasions we tracked birds in daylight. With 7 × 50 binoculars mounted on the antenna supports and aligned with the radar beam, we could see the bird in question if it was the size of a crow or larger. Crows, turkey vultures, and buteos were tracked in this manner to distances of about 1000 m. In daytime the radar would often track what seemed to be small birds, moving somewhat more slowly than the hawks, but these would often not be visible with the binoculars even when within 400 m range. This was partly due to the vibration caused by the autotracking mechanism. While we could not distinguish single birds from flocks with any great confidence, ornithologists experienced in observing migrants visually against the full Moon have the impression that most fly singly or in relatively dispersed flocks (ref. 9). Most of the radar targets we believe to have been birds had fluctuations of the echo amplitude similar to those described by Bruderer (ref. 10) and Bruderer and Joss (ref. 6). These became recognizable with experience and matched the fluctuation patterns when visible birds were tracked in daytime. This criterion is subjective and imprecise by itself (ref. 11), but we found it persuasive in practice. All targets discussed in this paper moved at groundspeeds appropriate for birds, and the times when they were most abundant were appropriate for spring migrants. All tracks were included in the analyses, provided that they were of sufficient length and free from various artifacts discussed below. When feasible, airspeeds were estimated from wind velocities determined by tracking a balloon at the same location. When we did not obtain local balloon tracks, we were obliged to use the radiosonde data discussed below. In most of the former cases airspeeds were clearly appropriate for birds, and unlikely for any other known types of targets such as insects or wind blown material. A complication arises, however, in cases discussed in a separate section of this paper in which birds appear to have spent considerable periods of time in almost stationary flight.

The arrangements for recording range and azimuth sometimes produced artifacts. The potentiometers generating the dc voltages proprotional to range and azimuth were attached to shafts that rotated once for each 1000-yd (944-m) interval of range and once per revolution of the radar in azimuth. Consequently the frequencies necessarily shifted from minimum to maximum or vice versa when a bird passed through switch-over val-

ues of range or azimuth. Occasionally a bird was so uncooperative as to remain for several seconds close to a switch-over point or even move back and forth across it. Since the computer counted the total number of waves within each 1 sec interval, each such crossing yielded intermediate values corresponding to erroneous positions of the bird. Such artifacts could readily be eliminated, with only small resulting gaps in the plotted tracks. Such gaps are shown in the figures with broken lines. It was also necessary to note in which 944-m range interval each bird was acquired by the radar. The computer program was then able to apply appropriate corrections when the range frequency passed either upward or downward across a switch-over point.

Many of the tracks recorded by our radar system were remarkably straight, but others showed various sorts of curvature, and a few involved many shifts in direction at close intervals. After considering several methods of expressing the degree of departure from a perfectly straight line, the following two were selected as most helpful for present pruposes: (1) a simple straightness index, and (2) the groundspeed ratio, or ratio of net to total distance travelled. The straightness index employed was the length/width ratio of the smallest rectangle that included all bird positions on the XY plot except those that were clearly due to artifacts. This is a conservative criterion, since the straightness index is lowered substantially by either a gradual curve or by one questionable point well off the straight line that best fits the great majority of the points. The groundspeed ratio was the straight line distance between beginning and end of the track divided by the total of the XY distances shown in the print-out for all the 1-sec intervals between bird positions calculated by the computer. Here too we excluded clearly erroneous points where range or azimuth frequencies passed through crossover points. The highest observed straightness indices were greater than 100, and the groundspeed ratio was often 0.98 or 0.99. This shows that radar artifacts did not add appreciably to the recorded length of the flight path.

Location of Radar Observations

Although a number of locations were utilized for preliminary observations, only two will be considered here: (1) The Bronx Zoological Park in the northern part of New York City (73° 52′ W. Long., 40° 52′ N. Lat.), close to the Bronx River and at an elevation of approximately 15 meters above sea level; and (2) Ice Caves Mountain, approximately 5 km southwest of Ellenville, N.Y. (74° 21′ W. Long., 41° 42′ N. Lat.). Here the radar was located at 670 m above sea level on a plateau that ranged between 600 and 700 m over an area of several square km. These two observation points are shown in figure 1, together with the airports from which meteorological data were obtained. The terrain was essentially level around the Bronx location, but heavily built up. There were steep hillsides within a few km of the radar location near Ellenville, and these could well have generated obstruction updrafts, as discussed below.

Meteorological Data

Since the basic purpose of these observations was to determine the relationship of the birds to cloud layers, all available meteorological data were obtained from the U.S. Weather Bureau and the Federal Aviation Agency stations in the New York area. Surface observations were available from 11 airports shown in figure 1. Radiosonde data were available at 12-hour intervals from J. F.

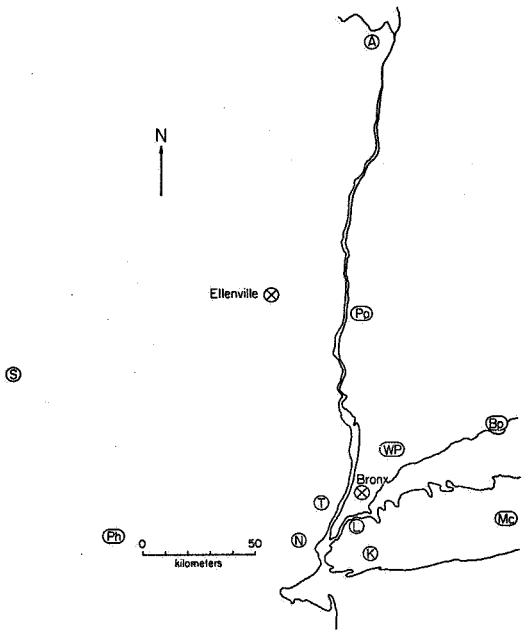

FIGURE 1. Location of radar and sources of meteorological data. A = Albany, BP = Bridgeport, K = Kennedy, L = LaGuardia, Mc = MacArthur, N = Newark, Ph = Phillipsburg, N. J., Po. = Poughkeepsie, S = Wilkes-Barre, Scranton, T = Teterboro, WP = White Plains.

Kennedy Airport, N. Y., and Albany, N. Y. These provided data on wind direction, windspeed, temperature, and humidity at the two airports when the radiosonde balloon ascended. Most of our observations were conducted within 3 or 4 hours after the evening radiosonde ascent (nominally at 0000 Greenwich Mean Time). Ellenville is approximately equidistant from New York and Albany, hence our estimate of Ellenville winds, temperatures, and humidities were made by proportionate interpolation according to the time and location of the observation. The Bronx location was much closer to Kennedy Airport, and Kennedy data were used to estimate wind and cloud conditions there.

We also attempted to obtain local wind data by tracking with the same radar a meteorological pilot balloon beneath which was suspended a radar target. Unfortunately operational difficulties prevented this from being accomplished on April 23 or May 16, 1970, which turned out to be two of the most interesting nights in terms of cloud depths. But on April 30, 1970, two balloons were tracked late in the evening, and these balloon tracks provided more accurate determinations of local windspeed and direction. Airplane pilots reported additional data concerning the upper limit of cloud layers which the Watch Supervisors of the New York Air Traffic Control Center kindly furnished to us by telephone. These were not as numerous nor as close to the location of our radar as would be ideal, but they provided valuable supplements to the other meteorological data.

To facilitate comparison with the directions in which birds were moving, all wind directions discussed below are the direction toward which the air was moving. Thus a north wind in ordinary usage is designated 180°.

RESULTS

Observations during certain nights in the fall of 1969 and the spring of 1970, other than the nights discussed in detail below, showed that many birds were migrating in approximately the appropriate directions under opaque layers of altocumulus or other types of cloud. We could not discern any consistent differences in the straightness of such tracks between overcast and clear nights. No tracks on completely clear nights were straighter than 2121 or 2134 of April 30. This could be interpreted as evidence that when flying under clouds but over well-settled land areas birds may orient by means of artificial lights on the ground. In all such cases lights were available in sufficient

abundance that a bird could probably maintain tracks as straight as we observed by selecting a light approximately straight ahead, flying toward it for a few minutes and then shifting attention to another, more distant, light in the same direction.

On the nights of April 23, April 30, and May 16, 1970, deep and continuous stratus clouds were present. Out of 73 birds tracked many were observed at altitudes that seem to have been well within the cloud layers. These data will therefore be presented in detail.

April 23–24, 1970, Bronx, N. Y.

Occluded fronts were located to the north, west, and south of the New York City area during this night with widespread low clouds and fog. All aviation surface weather observations from 2100 to 0000 at Kennedy, La Guardia, Newark, Teterboro, White Plains, and Bridgeport airports showed low ceilings, with overcast reported at altitudes ranging from 30 to 400 m. At 2000 La Guardia reported broken clouds at 390 m and overcast at 1220 m; Teterboro reported broken clouds at 340 m and overcast at 610 m. But at the other four airports overcast was reported at 370 m or lower at this time. The ceilings lowered throughout the evening, and after 2100 the highest at any of these airports was 300 m. From 2200 until after midnight the nearest airports all reported fog and ceilings below 150 m.

Figure 2 shows the radiosonde data from Kennedy Airport (30 km south of our location). At 1928 very moist air (dew point depressions less than 1.5° C) extended from 200 to 1850 m with a pronounced change to dryer air above this level. In the morning there were variable but relatively low dew point depressions (0.8° to 4.8° C) up to about 3000 m. The Albany radiosonde data also showed dew point depressions of less than 2° up to 1840 m in the evening and up to 880 m in the morning, with other high humidity readings in the morning above 3500 m. At Kennedy the radiosonde recorded a slight inversion from 200 to 1200 m and a nearly isothermal layer up to 2000 m, both evening and morning. At Albany the inversion was more pronounced and extended from 550 to 1500 m both evening and morning.

Five reports from airplane pilots were available during the time of our observations. Three were consistent with the Kennedy Airport radiosonde data in indicating the top of the cloud layer to be around 1800 m (1815 m at Bridgeport at 2030, 1815 m at Carmel, N. Y., 61 km north of the Bronx, at 1900; and 1720 m at 2100 near Northport, 37 km east of the Bronx). But two other pilots reported cloud tops at 1030 m—at White Plains at 2300 and at Bayville, N. Y., 26 km east of the Bronx at 1930. These reports indicate variability in the cloud tops, or possibly emergence of the pilot from one layer with other unreported clouds above his plane. But even the lowest of the five pilot's reports place the cloud tops above 1000 m. April 23 was two days past full moon; the moon rose at 2130 and set at 0628; and hence it was above

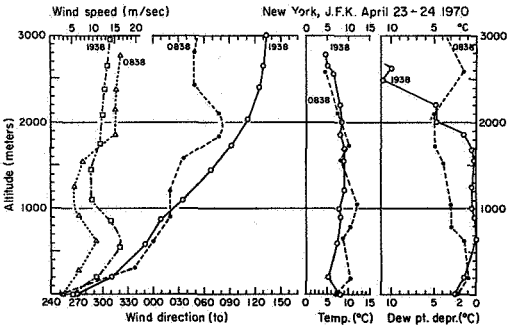

FIGURE 2. Radiosonde data from J. F. Kennedy Airport, April 23 and 24, 1970. Time, EST. Winds are shown as direction toward which air moved.

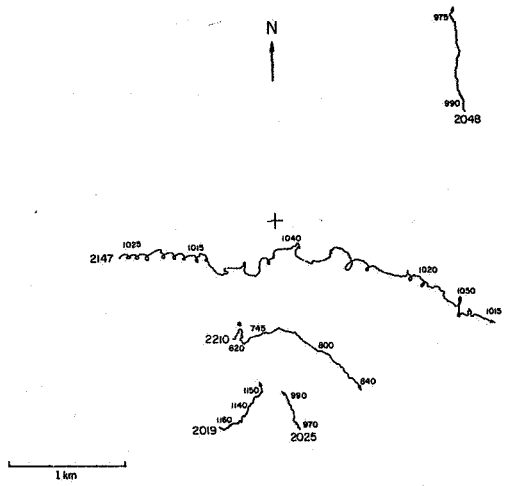

FIGURE 3. Radar tracks of birds over Bronx, N. Y., April 23, 1970. Cross near center is radar location. Number at start of each track is local time (EST) when tracking began; other numbers are altitudes in meters. Between numbers, changes in altitude were gradual and of roughly constant slope, within the radar accuracy. Dashed lines replace radar artifacts but with no sign that radar shifted targets. Asterisk indicates period of nearly stationary flight. A few tracks have been displaced slightly, relative to the radar, to avoid crossing other tracks.

the horizon when most of the birds were tracked.

Since we did not succeed in tracking a local balloon on this evening, our best data concerning local winds come from the evening radiosonde ascent from Kennedy Airport (fig. 2). The wind shifted markedly with increasing altitude from surface winds blowing towards 270° through 000° to 096° at 1760 m. The morning radiosonde at Kennedy showed very similar winds up to 1500 m except that the wind shear was considerably less, with surface winds blowing to 340°. Surface winds at the airports within a few miles of our observations were consistently light and blowing towards southwest or west throughout the period of our observations. At the altitudes where we tracked birds, the winds varied from about 000° at 500 m to about 090° at 1700 m. Thus many of the birds tracked were flying in crosswinds. Wind speeds varied in a moderatley complex fashion according to the Kennedy radiosonde data, increasing in the evening from 5 m/sec at the surface to 16 m/sec at 560 meters, then falling to 9.5 m/sec between 1100 and 1440 m followed by a gradual rise to 11.5 m/sec at 1780 m. In the morning the winds followed a similar pattern but windspeeds were only 0.5 to 0.6 times the evening values.

Twenty-five birds tracked between 2006 and 0003 EST yielded 17 tracks longer than 1 km, with the longest 4.36 km. But several shorter tracks are also included because of special features. These birds varied in altitude from 540 to 1775 m. Figures 3 through 7 show the tracks and altitudes of all birds except for a few where computer artifacts rendered the track very difficult to plot even though its general direction was evi-

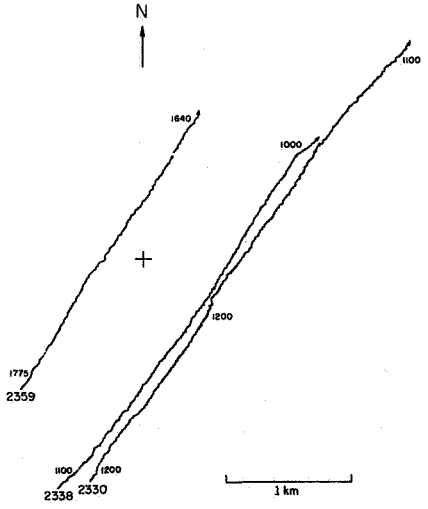

FIGURE 4. Radar tracks from Bronx, N. Y., April 23 and 24, 1970 (symbols as in fig. 3).

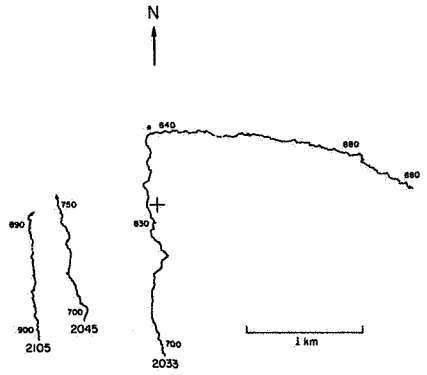

FIGURE 5. Radar tracks from Bronx, N. Y., April 23, 1970 (symbols as in fig. 3).

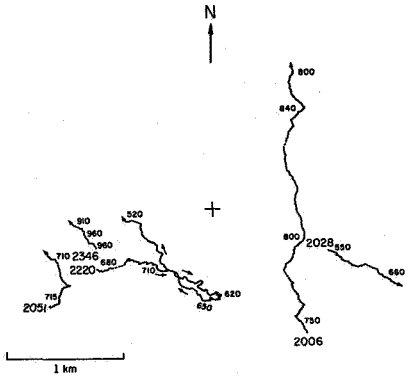

FIGURE 6. Radar tracks from Bronx, N. Y., April 23, 1970 (symbols as in fig. 3).

dent. Here and elsewhere it is convenient to identify each bird by the time when its track began. Three tracks showed such clear turns (2033, 2220, and 0003) that additional track directions were determined for the separate legs. The resulting 29 track directions vary from 315° (second leg of 2220) to 123° (2100), with an average of 035°. All 29 tracks were within 90°, 21 within 60°, and 16 within 45° of the mean. Thus these birds were reasonably well oriented for spring migration.

Many of these tracks were far from straight. The average straightness index defined above was 13.5 (2.35 to 44.6), and the mean groundspeed ratio was 0.72 (0.40 to 0.99). Birds such as 2147 and 2220 circled, looped, zigzagged, or flew in other patterns so that the total distance traveled was more than double the net distance covered. For example 2105 was followed over a total distance from beginning to end of the track of 1.09 km during 107 seconds which is equivalent to a net speed of 10.2 m/sec. But the average speed from the computer print-out was 16.0 m/sec (groundspeed ratio = 0.64), and close inspection of the track showed many small scale zigzags. A few shorter tracks

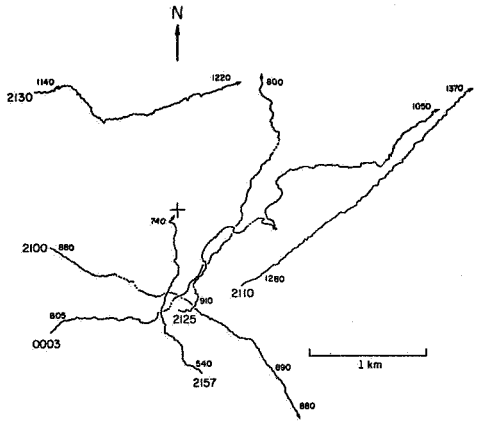

FIGURE 7. Radar tracks from Bronx, N Y., April 23, 1970 (symbols as in fig. 3).

showed even lower groundspeed ratios: 0.47 for 2051, 0.46 for 2346, and 0.40 for the most striking case of all, 2147, in which a total net track of 3.20 km required almost 10 minutes.

It seems unlikely that these non-linear tracks were operational artifacts of the radar, because very straight tracks and very irregular ones were registered within a few minutes. Rapid switching of the autotracking between members of a flock also seems an unlikely explanation, since the second-to-second speeds were reasonably consistent and in

some cases a definite but complex flight pattern was plotted. Clearly many of these birds were making extensive but small scale deviations from a perfectly straight track, while nevertheless maintaining a consistent direction of progress. A possible interpretation of such behavior will be discussed below. Estimates based on the evening radiosonde from Kennedy Airport indicated implausible airspeeds and headings on April 23. These do not seem meaningful in view of the differences on April 30 between Kennedy radiosonde values and local wind data obtained by tracking our own balloons.

On balance the available meteorological data point consistently toward the presence of a low-lying stratus cloud layer extending throughout the period of our observations from ceilings at 200 to 400 m up to cloud tops between 1700 and 2000 m. All birds we tracked were certainly above the cloud base, and appeared to be well within the stratus layer. At least half were below the lowest of five pilot's reports, which as mentioned above were not wholly consistent with the radiosonde data.

Night of April 30-May 1, 1970 Bronx, N. Y.

A very weak and ill-defined occluded front extended from north to south through the New York area with low stratus clouds and fog. Throughout the period of our observations Kennedy, Newark, Teterboro, La Guardia, White Plains, and Bridgeport observations showed either fog, indefinite low ceilings, or overcast at 60 to 250 m. Visibilities were virtually zero to not more than 3 km. Winds were light and blowing to about 315° to 000°. Pilot reports of cloud tops were available from several km north and east of the Bronx and ranged from 900 m to 1830 m. The radiosonde data from Kennedy Airport in the early evening showed an isothermal

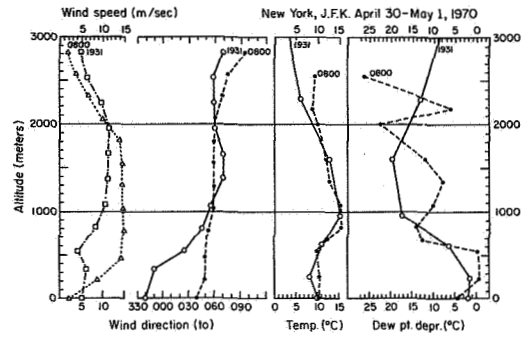

FIGURE 8. Radiosonde data from J. F. Kennedy Airport, April 30 and May 1, 1970. Time, EDST.

layer at approximately 10° C from the surface to 550 m and a marked inversion with temperatures of 16° between 800 and 1100 m (see fig. 8). Above this level the temperatures dropped gradually to reach 8° at approximately 2100 m. The humidity sensors in the radiosonde showed a very high humidity (dew point depression less than 2°) up to approximately 500 meters with very much dryer air at higher altitudes. This indicates that the stratus cloud did not extend above 500 meters, although the pilot reports indicated higher cloud tops. Yet it would clearly be unjustified to conclude that any bird flying any higher than 500 meters was cut off from a view of the sky.

The wind directions indicated by the evening radiosonde ascent from Kennedy varied from winds blowing to 340° at the surface shifting to 070° at 1400 m. We succeeded in tracking two balloons with our radar after our observations of birds, and these showed the local winds at 0033 and 0100 to be quite consistently toward 005° ± 10° up to an altitude of 900 m where both balloons were lost because of interfering buildings on the horizon. Windspeeds from these two balloon tracks, which were quite consistent, were 7 m/sec from 200 to 400 m, 11 m/sec at 400 to 550 m, 16 m/sec at 550 to 650 m, and 14

m/sec at 650 to 925 m. The wind data from Kennedy Airport radiosonde data (fig. 8) differed by as much as 40° in direction and up to 10 m/sec in speed from these local measurements. This difference demonstrates the importance of local and approximately simultaneous wind measurements for reliable estimates of a bird's airspeed and heading.

A conservative interpretation of these meteorological data indicates a continuous layer of low stratus cloud extending from 200 m or lower up to approximately 500 m. It was 9 days past full Moon and the Moon set at about 2200, so that it was not available during most of our observations.

Twenty-eight out of the 29 tracks obtained between 2121 and 0052 EDST were between 322° and 080°, with a mean of 026°. One track at 147° (2150) clearly lay outside the range occupied by all the rest. The altitudes of these tracks ranged from 230 to 1060 m. Of the 28 tracks between 322° and 080°, 25 were within 60° of the mean, 23 within 45°, and 16 within 30° of the mean. All tracks are shown in figures 9 to 12.

Those tracks that were above 500 m were distinctly straighter than the four tracks that were clearly below this cloud top level, as indicated by the radiosonde data of figure 8 (2150, 2240, 2303 and 2306, all shown in fig. 9). The first was short and highly non-linear, with a straightness index of 4.3 and a groundspeed ratio of 0.36. Furthermore the track direction was 147°, and the heading calculated from local wind data was 178°. This bird's airspeed appears to have been 13.2 m/sec, based on its net track. But of course the actual integrated airspeed over the many changes of direction must have been considerably greater. The two tracks at 2303 and 2306 were also very far from straight, with straightness indices of 9.1 and 10.6 and groundspeed ratios of 0.57 and 0.49, respectively. Both track directions were 350°, and the estimated headings were 230° and 223°. Because these two targets were moving so

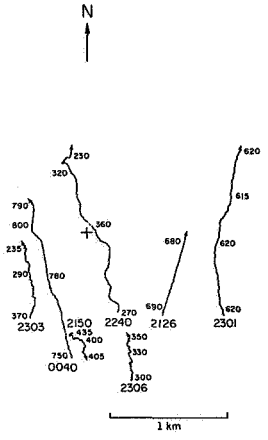

FIGURE 9. Radar tracks from Bronx, N. Y., night of April 30, 1970 (symbols are same as in fig. 3). Headings and airspeeds in m/sec estimated from local balloon tracks: 2150: 178°, 13.2; 2240: 316°, 5.8; 2301: 029°, 7.6; 2303: 230°, 2.2; 2306: 223°, 2.4; 0040: 318°, 11.8.

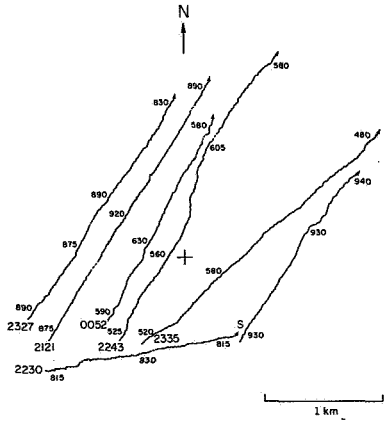

FIGURE 10. Radar tracks from Bronx, N. Y., night of April 30, 1970. S = shift of targets; other symbols as in figures 3, 8, and 9. 2121: 060°, 12.8. 2230 (1st bird): 140°, 15.8; (2nd bird): 080°, 9.6. 2243: 040°, 13.6. 2327: 064°, 12.6. 2335: 080°, 14. 0052: 057°, 13.4.

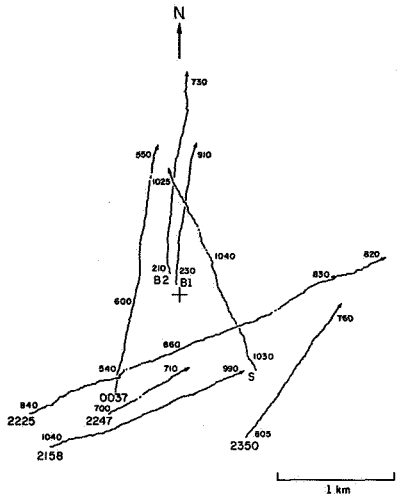

FIGURE 11. Radar tracks from Bronx, N. Y., night of April 30, 1970. Tracks B1 and B2 are balloons released at 0033 and 0100, respectively. Other symbols are as in figures 3 and 9. 2158: 117°, 17; 2225: 131°, 13.5; 2247: 122°, 12.6; 0037: 012°, 11.8.

nearly downwind, their indicated airspeeds were only 2.2 and 2.4 m/sec. This sugggests either that they were insects, or hovering birds, or something moving more slowly than birds, that their turns were even more extensive than indicated by the groundspeed ratios, or that the wind velocity was appreciably different from the winds measured with our balloons 1½ and 2 hr later. In contrast to these non-linear tracks below 500 m, 15 tracks between 500 and 700 m showed an average straightness index and groundspeed ratio of 32.7 and 0.94. For 11 tracks between 750 and 1050 m these values were 49.2 and 0.92.

Track 2240 was the longest within the cloud layer, and it was in an appropriate direction for spring migration (343°). Based on our local wind data, its airspeed was 5.8 m/sec and its heading 316°. This bird's straightness index was 10.1, and its groundspeed ratio was 0.80. The latter value probably means that the actual airspeed was above 10 m/sec when integrated over the several turns evident in figure 9. Estimates of this bird's airspeed, based on the local balloon tracks about 2 hr later, lead to distinctly different headings and air speeds during different portions of the curving flight path shown in figure 9. From 14 to 48 seconds after the radar was locked onto this bird its track was almost exactly 000°, its groundspeed averaged 13.8 m/sec, and estimated heading and airspeed were 355° and 6.8 m/sec. It then turned left with absolutely no sign that the radar shifted to a different target and moved between 49 and 75 sec with a track direction of 320° and an average groundspeed of 14.6 m/sec. This northwesterly leg involved a heading of 293° and an airspeed of 10.8 m/sec according to our local wind data. This is consistent with the reports of Bellrose (ref. 12) and with the recent findings of Bruderer and Steidinger[1] that birds lower their airspeeds in tail winds. But perhaps the most appropriate conclusion to be reached from these data is that calculations of a bird's airspeed and heading should not be taken very seriously unless local wind data are obtained at the same place as the radar tracking data and within a few minutes of the same time. Particularly under conditions of wind shear and complex air movement, local winds may well vary considerably from moment to moment.

On balance there is thus a clear indication on the night of April 30 that those birds flying in the stratus cloud layer were deviating distinctly more from a straight flight path than those that were above the cloud tops. Nevertheless three of the actual tracks of these birds flying in the cloud layer were rea-

[1] See paper by Bruderer and Steidinger in this volume.

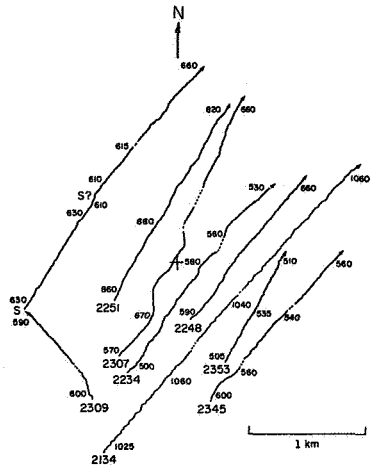

FIGURE 12. Radar tracks from Bronx, N. Y., night of April 30, 1970. Symbols are as in figures 3 and 9. 2134: 073°, 14.6; 2234: 082°, 7.8; 2248: 129°, 8.8; 2251: 057°, 13.0; 2307: 105°, 6.0; 2309: 247°, 11.4; 2345: 084°, 13.6; 2353: 044°, 15.6.

sonably appropriate for seasonal migrating (343°, 350°, and 350°), while the fourth had a quite inappropriate migration direction of 147°.

May 16-17, 1970, Ellenville, N. Y.

A cold front was approaching from the west and passed approximately over our location in the early morning shortly after our last observation. There was widespread low stratus cloud and also very high rows and cells of convective cloud with heavy showers and thunderstorms. The weather bureau radar in New York City showed bands of radar reflective clouds with large water droplets moving from west to east toward and through the Ellenville area throughout the night. The tops of these cumulus clouds were at 9000 to 10 000 m, but this type of radar does not reveal stratus clouds and consequently tells us nothing about the tops of the clouds that lay between the bands of thunderclouds. Shortly after we arrived on the plateau, very thick fog descended and remained throughout the night. In the early morning as we drove down from the plateau, we did not emerge from the bottom of this stratus layer until we were at least 200 m below the radar.

Surface observations at Binghamton, N. Y. (140 km west of Ellenville), Newark, Teterboro, White Plains, and Poughkeepsie showed overcast throughout the night at altitudes lower than our radar. The New York City airports, Wilkes Barre—Scranton, and Albany also showed continuous overcast, although at times it was above our altitude. Because the weather was so bad, no pilot reports were available from anywhere close to our area during the night.

The radiosonde data from both Kennedy Airport (fig. 13) and Albany (fig. 14) showed virtually saturated air (dew point depressions 2° C or less) from well below the altitude of our radar up to 2000 m. There was also some indication of higher clouds, but it seems conservative to assume that birds flying within range of our radar must have encountered stratus clouds from below our altitude up to about 2000 m above sea level.

There was heavy but intermittent rain during the night, and the 3 cm radar itself showed much cloud echo when used at low

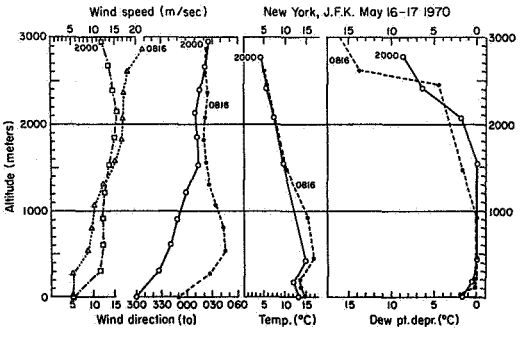

FIGURE 13. Radiosonde data from J. F. Kennedy Airport, May 16 and 17, 1970. Time, EST.

elevations. We searched for birds from 2030 to 0320 EDST, whenever it was not actively raining. There were many fewer birds than on April 23 or April 30, but during this period of about 7 hr we tracked 21 for distances ranging from 200 to 3680 m. On many other occasions what appeared to be a bird would be observed on the A-scope, but it would prove impossible to maintain it for more than a few seconds in the autotrack mode. Hence several relatively short tracks are included in figures 15 to 17. It seemed likely that the many failures to track birds were due to interfering echoes from the clouds, although this cannot be established with certainty.

Since we were in thick fog we could not manage to locate a balloon in order to lock the radar on to it. Wind direction at the altitudes where we tracked birds can be estimated only from the New York and Albany radiosonde data. The evening radiosonde ascents showed almost identical wind directions at these two stations, 350° at 1000 m shifting to approximately 025° at 2400 m. At both stations the winds at lower elevations showed a clockwise shift during the night. A reasonable average interpolated value of wind direction would appear to be 020°, and the maximum discrepancy from this interpolated average

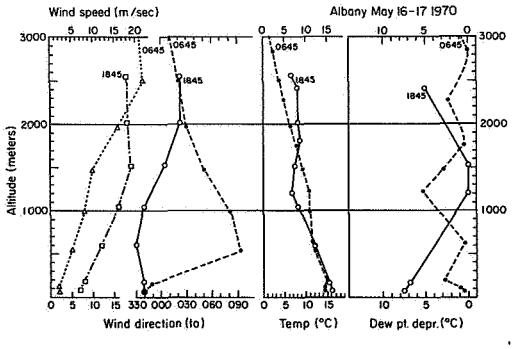

FIGURE 14. Radiosonde data from Albany, N. Y., May 16 and 17, 1970. Time, EST.

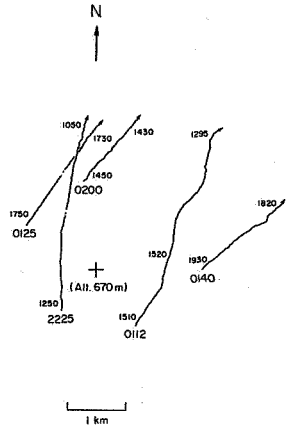

FIGURE 15. Radar tracks over plateau southeast of Ellenville, N. Y., May 16 and 17, 1970. Time, EDST; symbols as in figure 3; altitudes are above sea level; radar location is at 670 m.

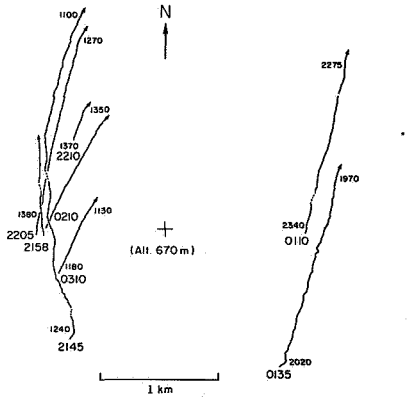

FIGURE 16. Radar tracks near Ellenville, N. Y. Symbols are as in figure 3. Altitudes omitted to avoid crowding: 2158: 1240 to 1100 m; 0210: 1170 to 1110 m.

wind at either airport, morning or evening, at the altitudes where birds were observed was only about 40°. The windspeeds were reasonably consistent for the four radiosonde ascents at New York and Albany, and an interpolated value of 12 m/sec at 1000 m rising to 17 m/sec at 2400 m seems a reasonable approximation. It was 5 days before full Moon,

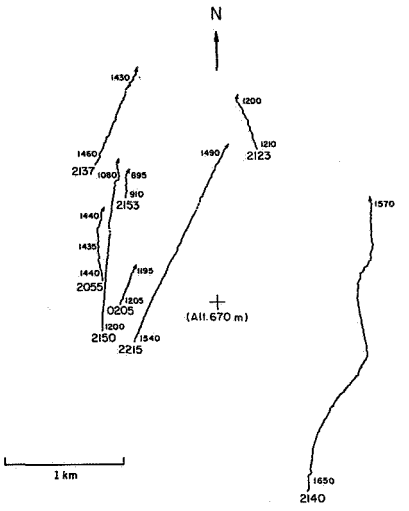

FIGURE 17. Radar tracks near Ellenville, N. Y. (symbols are as in fig. 3).

but the Moon set about 2230 and hence was unavailable for most of the night.

The 21 birds tracked were much more consistent in track direction than on any other night when extensive data were gathered. The average track was 016° (340° to 050°). All tracks were within 45° of the mean and 19 out of 21 were within 30°. All the birds tracked were flying very nearly downwind, and their groundspeeds ranged from 20 to 37 m/sec with the higher groundspeeds being those of birds at higher altitudes, as would be expected. All tracks were quite straight with practically no deviations of the types so prominent on April 23rd and below 500 m on April 30th. The straightness index varied from 8.75 to 91.3 (av 30.15), and the groundspeed ratio averaged 0.93 (0.88 to 0.99). Unless the New York and Albany radiosonde data were grossly misleading with respect to our location, the majority of these birds must have been migrating within the stratus layer with no opportunity to see sky or ground. The possible role of obstruction updrafts will be discussed below.

"Stationary" Flight

A few of the tracks recorded by our radar showed periods of several seconds during which the X, Y, and Z coordinates remained almost unchanged. If a target did not move when first acquired, we would ordinarily assume it was some peculair form of ground echo. Such stationary targets were observed in many locations, but they were especially common in the Bronx. They could be identified as fixed targets because some had the azimuth of prominent buildings and because the radar would remain locked on to them indefinitely, giving constant values of azimuth, elevation, and range. They were much more common at low elevations, but some would be found consistently from night to night in the same location, and these appeared to be reflections of side lobes of the radar beam from buildings, even though the elevation was much too high for the building in question to lie in the main beam. But what will be called here for convenience "stationary birds" were clearly distinguishable from such fixed ground targets because they moved at speeds appropriate for birds before and/or after a period when the radar coordinates remained approximately constant. The following specific cases on April 23 in the Bronx demonstrate this phenomenon most clearly.

The bird tracked at 2033 (fig. 5) was unusual in making a gradual turn of about 90° at 200 to 205 sec after tracking began. Unlike many other tracks with pronounced turns, there was no sign that the radar had shifted to another bird—such as a discontinuity in altitude or an unusually high XY speed registered near the time of the turn. The average groundspeed was 8.2 m/sec during the first leg and 6.7 m/sec during the second leg when the bird moved roughly east. The altitude rose very slowly and gradually with minor variations during this long track from

700 to 835 m, and between 170 and 235 sec it varied only between 831 and 846 m. Shortly after the 90° turn, at the point marked with an asterisk in figure 5, the bird's position remained stationary for 7 sec, all points in that interval falling within a horizontal area of 5 × 11 m and a vertical range of only 6 m. This is approximately the accuracy of the radar. Yet immediately before and after this stationary period the track showed regular horizontal motion at speeds typical of the rest of the track with no sign that the radar switched to a new target. The winds at the bird's altitude, according to the Kennedy Airport radiosonde less than an hour earlier, was blowing to about 005° at about 12 m/sec. This wind velocity would mean that during the first leg the bird was heading about 191° and flying at an airspeed of about 5.5 m/sec, in other words being blown backwards at double its airspeed!

After the turn the estimated airspeed and heading become 15.6 m/sec and 164°. During the first leg the groundspeed ratio was 0.71 and the straightness index 9.4, indicating, as is clear from figure 5, that the track was deviating considerably from a straight line.

A second and even more striking case was the bird tracked at 2210. For the first 2 minutes of tracking it remained within an area about 100 meters square, marked with an asterisk in figure 3. While the indicated position moved back and forth irregularly during the first 2 minutes, there was a 20 sec period during which all recorded positions fell within a 20 m square horizontally while the altitude varied irregularly over a total range of only 23 m. During this period the bird gained considerably in altitude, rising from 620 to 710 m. Then without any indication that the radar had switched to a new target it moved off on a somewhat irregular southeasterly course with a gradual curve, covering 1440 m horizontally in 153 sec while climbing about 135 m. Judging by the radiosonde data, this bird also faced into a 12 m/sec wind blowing toward the north during its first 2 min of climbing with virtually no horizontal progress. Its subsequent movement along a curved path was also studded with short zigzags, and the groundspeed ratio was only 0.61. Its indicated airspeed and heading during this time were 16.8 m/sec and 174°. Both these birds might have been flying in tight circles or other small scale patterns not accurately plotted by our radar, and we cannot be certain that the radiosonde data are accurate for the air in which these birds were flying.

DISCUSSION OF FINDINGS

Although many of the weak, low velocity radar targets that used to be considered mysterious "angels" have been accounted for by evidence that they are birds or insects, there remain others that have been explained, with some difficulty, as meteorological phenomena (ref. 13). It is often taken for granted that if a target is stationary or moves at the estimated velocity of the local wind it cannot be a bird. The two cases discussed in the previous section, and others for which the evidence is not so complete, were apparently birds that spent a considerable period of time almost stationary. But of course we have no way of knowing whether they were soaring in circles of small radius, hovering, executing small scale and rapid zigzags, or employing other types of flight behavior. It is even possible that flight patterns not ordinarily seen in daytime may be used when flying among clouds at night.

A final possibility that seems worthy of consideration is that some form of dynamic soaring was being practiced by the birds which indulged in so many rapid, small scale

changes in direction of flight. Our computer program calculated the position of each radar target only once per second, so that very rapid changes in heading would not have been detectable. The fact that some birds changed course so frequently, sometimes in fairly regular patterns, suggests that further detailed observations might disclose some pattern of dynamic soaring such as those suggested long ago by Breguet (ref. 14).

Unfortunately on April 23 we did not obtain data on winds from local balloon tracks, and the differences between these local data and radiosonde data from Kennedy Airport on the night of April 30 warn us not to rely too heavily on the latter for estimating airspeeds and headings of birds tracked 30 km away. Hence we can only speculate about the patterns of air movement in which these birds were maintaining almost stationary flight. But figure 2 shows that on April 23 there was considerable wind shear and probably convective currents inside the stratus layer where these birds were apparently flying. Other birds such as 2125, 2147, and 2220 of April 23 were also flying in very complex patterns. It is, therefore, tempting to speculate that some of these birds were riding updrafts in ways roughly similar to the soaring flight of hawks, gulls, or vultures in daytime under cumulus clouds or along ridges.

Bellrose (ref 12) reports a puzzling variation in airspeeds of nocturnal migrants flying in various windspeeds and directions. While only average values are presented, they indicate that birds tended to maintain a constant groundspeed, flying at lower airspeeds in tail winds and vice versa. While it is difficult to make direct comparisons between Bellrose's data and ours, the complex tracks described above would appear as very slowly flying birds if one could not plot the fine details of each flight path. Particularly when flying inside stratus clouds, birds may alter their flying tactics to take advantage of rising currents at some sacrifice in groundspeed, as speculatively discussed elsewhere (ref. 2).

Finally we must ask whether the meteorological data discussed above are adequate to establish whether or not the birds tracked on the nights of April 23, April 30, and May 16 were in fact inside of opaque clouds. Cloud layers are well known to have gaps, to be variable in thickness, and to have both tops and bottoms that deviate considerably from a horizontal plane. The possibility that extensive gaps occurred in the cloud layers on these three nights can be discounted to a considerable degree by our own local observations. One of us looked carefully at close intervals for any signs of stars, or the Moon when present. No such indications of breaks in the cloud layer were seen during the periods of observation described above. Since our radar was limited in its range, it seems unlikely that there were holes in the cloud where any of the birds we tracked were flying. Furthermore the bottoms of the clouds were in all cases visibly low, and on the night of May 16 unquestionably well below the altitude of the radar.

The only serious doubts about the adequacy of our meteorological data concern the tops of the cloud layers, which were of course invisible to us. The principal evidence about cloud tops was the radiosonde data indicating layers of nearly saturated air up to certain altitudes. But these samplings of the atmosphere occurred at different times and places from our radar observations. Thus it is always possible that the birds we tracked were flying through local depressions in the cloud tops. It seems highly unlikely, however, that under the conditions prevalent on these three nights the cloud top level would have been below the altitudes indicated by radiosonde data for extended periods. Had the stratus clouds

been this variable, the ceilings would probably have varied more than they did at the six neighboring airports from which reports were obtained, and stratus clouds of highly variable thickness would probably also have presented occasional breaks through which we could have seen the Moon or stars.

Nevertheless it is quite appropriate to be skeptical of evidence that birds can maintain reasonably accurate orientation without visual cues, in view of the evidence that Sun- and star-compass orientation is well within the capabilities of birds. Conservatively we might assume that the stars or Moon were visible to all birds above 500 m on April 30 and even to those above 1000 m on April 23 (on the basis of pilots' reports of cloud tops well below the level where the radiosonde data showed a marked change from moist to dry air). We might further assume that over the plateau, where our radar was located on May 16 and 17, there were strong ridge updrafts in which the birds were riding and maintaining straight tracks by sensing the wind direction from turbulence patterns despite the stratus cloud. The only steep hillside within range of our radar was about 1 km to the west where the ridge was approximately parallel to the wind direction and hence not likely to produce a consistent updraft. Many birds were flying roughly over this steep hillside, but others were not, as shown in figures 15 to 17. One can speculate from the topographic map (Napanoch quadrangle, U.S. Geological Survey 7½-min series) that these birds were riding updrafts from the steep cliffs running approximately southwest-northeast that are located about 2 to 3 km south and southeast of our location. But the topography appears equally suitable to generate updrafts in other areas within range of our radar where no birds were tracked. In short, strong ridge updrafts were undoubtedly present in the area, but no convincing correlation is evident between topography and the bird flight paths actually observed.

Even granting these conservative assumptions, there remain at least 15 to 20 birds tracked over the Bronx on April 23 and 30 that appear to have been well within the stratus cloud layer. In the Bronx there are no topographic features adequate to provide orienting updrafts at altitudes of several hundred meters. Chimneys could well have provided artificial thermal updrafts, but we could discern no correlations between specific buildings and the flight paths of those birds tracked on April 23 and 30 that appear to have been inside the clouds. Many were flying over the Zoological Park or Botanic Garden which have no large heat sources. This part of the city does not have large power plants or factories that operate at night, so that this type of patterned updrafts does not seem likely.

It thus seems probable that these birds tracked within stratus cloud layers were using one or more of the non-visual mechanisms of orientation which I have recently discussed elsewhere (ref. 2). But descriptive observations of flight paths can scarcely tell us which sensory mechanisms of orientation were employed, except that some of the non-linear tracks suggest soaring on updrafts.

SUMMARY

1. Detailed flight paths of migrating birds on nights with widespread low stratus cloud were measured with a tracking radar during the spring of 1970. Each bird's position was continuously recorded within 5 ± 10 m. Meteorological data showed that on three nights stratus cloud was continuous throughout the area during the hours when birds were being tracked.

2. On these three nights many birds were tracked for distances up to 3 or 4 km at

altitudes that seemed to be occupied by opaque cloud layers, judging by surface observations, radiosonde data, and airplane pilots' reports. It is difficult to escape the conclusion that these birds were unable to see the sky or the ground. Nevertheless almost all were migrating in appropriate directions.

3. Some tracks of birds apparently within the stratus layers were reasonably straight and level, others were climbing or descending. Several were highly non-linear with zig-zags, curves, reverse turns, and in one case a series of loops similar to the path of a hawk soaring on updrafts from a ridge. These birds may have been using convective patterns of air flow within the stratus cloud.

4. A few radar targets that gave every evidence of being birds remained almost stationary for many seconds while apparently located within the stratus cloud. The wind was strong enough that this must have required heading into the wind. Before or after such a period of near stationary flight these birds moved progressively in a reasonably appropriate direction for spring migration. Such non-linear flight paths may account in part for some previous observations of "angels" that do not move as fast as typical birds. Previous reports of migrants flying at surprisingly low airspeeds may be birds flying in non-linear patterns adapted to take advantage of updrafts. But local winds should be measured directly and at the same time birds are tracked before confidence can be placed in calculated airspeeds of birds flying in air that is moving in complex patterns.

ACNOWLEDGMENTS

Lawrence Eisenberg of the Rockefeller University Electronics Laboratory and his staff selected, maintained, and modified the radar and designed auxiliary circuits for recording and analyzing the data. Richard L. Penney collaborated in all phases of the work, but it was in the area of operational logistics and field work that his work was especially vital. Donald K. Riker prepared the computer programs with collaboration from Robert Schoenfeld, Director of the Electronics Laboratory. Helen Hankin carried out much of the computer work and data analysis. Field work with the radar involved especially active participation by Ronald Larkin and by Charles Walcott and Jon Harris of the State University of New York at Stony Brook. I am grateful to the U.S. Weather Bureau for supplying pertinent data, and to the New York en route center of the Federal Aviation Agency for obtaining pilots' reports of cloud tops. V. Cardone of the Department of Meteorology, New York University, provided invaluable advice concerning the meteorological data and their interpretation. The work was supported by the National Science Foundation through grant GB7155. Without all these manifold contributions these observations could not have been carried out successfully.

DISCUSSION

CARR: On some of your tracks the zig-zags and loops seem to be a bit more regular than you would expect from pure chance. They have a certain periodicity about them. Have you considered the possibility that perhaps this reflects correction on the part of the bird?

GRIFFIN: I have thoughts about this, but they are purely speculative with no data. It is conceivable that these birds in the cloud are, in fact, getting some lift or at least some directional information from turbulence. I don't have any data as to just how turbulent the air was except on the night of the 30th with the balloon tracks, and then there was not any support for any very great turbulence. It is, however, an interesting thought.

CARR: Do you think that there was any periodicity at all or were they all completely random?

GRIFFIN: Some of them looked quite periodic. I am quite sure they were not random. It looked as though the bird was first making mild turns one way and then another, but we need more data.

GAUTHREAUX: On the particularly erratic tracks, what is the probability that you were not tracking a bird but tracking a bat?

GRIFFIN: It was too early and too cold for bats in New York. The most erratic ones were April 23. It was earlier than one sees bats. I have worried quite a bit about whether these things are all birds. I think probably they are. Furthermore, in the spring they are mostly going north and in the fall they are mostly going south. This rather circum-

stantial evidence makes it rather likely that most of them, at least, are birds.

WILLIAMS: Can we rule out red bats?

GRIFFIN: We can't entirely, but bats are not nearly as numerous.

SCHMIDT-KOENIG: Has anyone seen radar evidence or other evidence on dragonfly migration?

GAUTHREAUX: There are dragonfly movements that are detectable on radar. They appear on the radar screen as bands extending for several miles and perhaps half a mile wide. If one looks up with a 30-power telescope, one sees literally hundreds of dragonflies in a band flying at great altitudes. The bands are oriented with the wind, and the radar display is very different from those produced by migrating birds.

GRIFFIN: What was the spacing and were the conditions favorable for roll vortices?

GAUTHREAUX: Roll vortices could very well be involved. The bands of dragonflies might coincide with rows of updrafts, but I do not have the necessary data to show this. The spacing of the bands is on the order of perhaps 2 or 3 miles based on measurements taken from the radar screen.

WILLIAMS: In our work in Texas we found that the bulk of the insects were well below 500 meters. There were very few insects at the same heights as migratory birds.

David Wingate in Bermuda has been compiling the dates of major arrivals of birds as well as insects on Bermuda. He finds that there are quite often huge numbers of one or two species of butterflies or moths that arrive suddenly on the islands.

EMLEN: I would like to comment that radar tracking of birds already aloft will not allow us to determine whether birds merely maintain a bearing under overcast conditions (that they may have selected previously when other navigation cues were available) or whether the birds have the ability to determine a goal or compass direction under overcast. This is an important distinction. I feel that the question can best be resolved by radio- or radar-tracking individual birds that the experimenter releases from the ground. In this way, the actual decision making process at the initiation of a migratory departure can be studied. This should constitute a powerful technique for future studies, since the experimenter can control the cues available to the departing bird by selecting to release birds under specific meteorological conditions and by experimentally modifying the sensory capabilities of the migrants prior to their release.

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Session IV

Bird Migration and Homing

Chairmen, CHARLES WALCOTT, HELMUT E. ADLER

The Ontogenetic Development of Orientation Capabilities

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THE COLLECTION OF PAPERS presented at this symposium attests to the interest that problems of animal orientation have aroused in both physiologists and ethologists. One phase of orientation research, however, has received little mention. This is the question of the ontogenetic development of orientation capabilities.

Early field observers reported that among many species of birds (primarily shorebirds) the young migrate southward independently of adult conspecifics, hence orienting correctly without any prior migratory experience. As a result of such findings, migratory orientation became a classic example of an "innate" behavior (refs. 1 to 4). Unfortunately, this rather arbitrary labeling discouraged further research on the actual maturation of navigation behavior.

Actually, field experiments conducted over a decade ago suggested a dichotomy of navigation capabilities between young and adult birds. When birds of several species were captured and displaced from their normal autumnal migration routes, the adults appeared to correct for this displacement and returned to the normal winter quarters while immatures (birds on their first migration trip) did not, but rather took up courses parallel to the original direction of migration (refs. 5 to 8). This implies an improvement in navigation performance as a result of previous migratory experiences.

I arrived at a somewhat similar conclusion from studies of the migratory orientation of caged indigo buntings. Several years ago I naively was trying to locate the critical star pattern for celestial orientation in this species. My approach was to remove portions of a planetarium sky and look for disorientation among the birds. The results (ref. 9) demonstrated a high degree of redundancy in the celestial orientation system; different individual birds employed different "strategies." Thus one bunting required the entire area within 35° of Polaris for successful orientation while another individual required only a small portion of that circumpolar area. For one additional bird, the northern stars were not essential at all. Such results suggested a level of individual variation hard to reconcile with the idea of a predetermined star map under rigid genetic control.

These considerations have led me to study

TABLE 1.—*Orientation of Young Indigo Buntings, Hand-Raised Under Conditions of Visual Isolation from Celestial Cues, 1965*

Bird	No. of experiments	Units of activity (Total N) [a]	p (Rayleigh test)	p (V test)	Mean direction
w88		211	0.18	0.03	187°
	8		0.24	0.07	(152°)
w89		480	0.55	0.21	.....
	9		0.44	0.20	.....
w93		119	0.04	0.01	158°
	6		0.23	0.05	168°
w94		754	0.45	0.18	.....
	12		0.45	0.11	.....

[a] Sample sizes were determined by dividing the total number of units of footprint activity, N, by a correction factor. This divisor was determined empirically and represents the interval at which activity measures become independent of one another.

the orientational capabilities of hand-raised indigo buntings. This paper represents a summary of all such experiments performed to date. Portions have been adopted from studies already published (ref. 10) or currently in press.[1] I am grateful to the National Institutes of Health (through a health science advancement award to Cornell University) and the National Science Foundation (through GB 13046 X) for financial assistance. I also thank Margaret Platt and Carol Conley for help with experimental series II and III, and members of Cornell's Orientation Seminar Group for comments and criticisms.

METHODS

Two groups of buntings have been reared for experimentation, 10 individuals in 1965, and 26 in 1968. All birds were removed from their nests and brought to the laboratory where their visual experience with celestial cues was carefully controlled. I attempted to take birds before their eyes had opened, but this was not always possible. Details concerning the age, sex, fledging date, and "eye condition" of all experimental birds are given in Appendixes 1 and 2. Young birds were kept in nest-cups and fed a diet of cricket abdomens supplemented by several insectivorous mashes. At the time of fledging (when 10 or 11 days old) I transferred the birds to cages 65 × 65 × 65 cm (2 × 2 × 2 feet) in size. The diet gradually shifted to one of dried seeds and the buntings became self sufficient at an age of approximately 25 days.

Birds were housed in windowless rooms where the day length was controlled to duplicate that present outdoors. The young were maintained in both visual and acoustical isolation from adult indigo buntings (with the exception of experimental series IV). These studies, therefore, test only the effects of visual exposure to certain cues. The role, if any, normally played by the parents or other adult birds in influencing the orientational choices of immatures remains a subject for future investigation.

[1] EMLEN, S. T.: Celestial Rotation: Its Importance in the Development of Migratory Orientation. Science, vol. 170, Dec. 11, 1970, pp. 1198–1201.

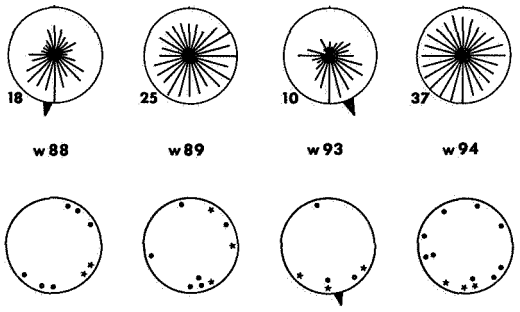

FIGURE 1. *Zugunruhe* orientation of young indigo buntings hand-raised under conditions of visual isolation from celestial cues and tested outdoors under natural night sky. Top: Vector diagram summaries plotted such that radius equals greatest number of units of activity in any one 15° sector. Number represented is at lower left of each diagram. Bottom: Distributions of mean directions for each bird. Stars represent mean headings for first three nights of testing. (Fewer than three stars indicates bird was inactive during early experiments.) Arrows denote statistically significant mean directions.

Weight, fat level, and molt status were recorded weekly for each bird. Nocturnal activity also was monitored. When the birds completed the postjuvenal molt, acquired visible subcutaneous fat deposits, and exhibited nocturnal activity, I considered them ready for experimentation. I placed each bird in an individual, circular, funnel-shaped cage, and recorded its directional tendencies by means of the "foot print technique" (ref. 11). In experimental series I, birds were tested outdoors under the natural night sky at a location 39 km (24 mi) from any sizeable town. This minimized the possibility of artifact orientation caused by horizon glows from city lights. Experimental series II, III, and IV were performed under the artificial skies of Cornell's research planetarium. This is an air-supported structure, hemispherical in shape, and measuring 9 meters in diameter and 5.5 meters in height. It is equipped with a highly modified Spitz Model A–3–P star projector. All planetarium settings were for a latitude of 42° north.

The results from each individual bird are presented both as a summary vector diagram and as a plot of the mean directions obtained from replicate tests. I tested the null hypothesis of randomness by both the Rayleigh test and the "*V*" modification of the Rayleigh test (ref. 12). Mean directions were calculated by vector analysis (ref. 13). Values for these statistics are presented in the accompanying tables. Unless stated otherwise, the figures are drawn with 0 or 360° representing north, 90° east, 180° south, and 270° west.

RESULTS

Experimental Series I

In the autumn of 1965, I tested the orientational abilities of 10 immature indigo buntings that had been hand-raised under conditions of restricted access to celestial information. These experiments have been reported upon elsewhere (ref. 10), and will be reviewed here only briefly.

Four individual birds lived in a windowless room from the time they were taken as nestlings until mid-September when they were tested outdoors under the natural night sky. During the experiments, they were placed outdoors after sunset and returned to their rooms prior to sunrise. Consequently the birds were never allowed a view of the Sun and were denied access to nocturnal celestial information until the migration season. Two experiments of approximately three hours duration were conducted each night, the first between 9 p.m. and midnight and the second from 1 to 4 a.m. As a result, these birds viewed a 105° rotation of the night sky during the experiments.

The results of these birds are shown in figure 1 and table 1. Using the "*V* test" for

TABLE 2.—*Orientation of Immature Indigo Buntings Allowed a One-Month Exposure to Natural Surroundings (Including Celestial Cues) Just prior to the Autumn Migration Season*

Bird	No. of experiments	Units of activity (total N)	p (Rayleigh test)	p (V test)	Mean direction
w95		73	0.00	0.00	192°
	4	insufficient sample size			(189°)
w96		819	0.00	0.00	186°
	13		0.15	0.00	166°
w97		191	0.08	0.01	184°
	3	insufficient sample size			(180°)

randomness, two birds are seen to show southerly tendencies. (Only w93 is significantly non-random by the Rayleigh test.) Considering the consistency of orientation during consecutive tests, only w93 shows a significant directional preference and then only by the "V" test. The behavior of the remaining birds was random.

A second group of buntings was given greater exposure to celestial information. Until self-sufficient, they were raised by a colleague, John Rice, who housed them in a room with a south-facing window. Although they were covered at night, they frequently were able to observe the daytime sky and, occasionally, the Sun itself. I obtained these birds shortly after their fledging and moved them to the windowless room where they lived until August 15. I then placed them in a large outdoor aviary for a one month period prior to the migration season (August 15 to September 15). This aviary allowed a full view of the sky and natural surroundings. The results from these birds, presented in figure 2 and table 2, show a notable improvement over the previous group. All three birds displayed clear southerly tendencies; the consistency of these directional responses, revealed by the nightly mean headings, also improved considerably.

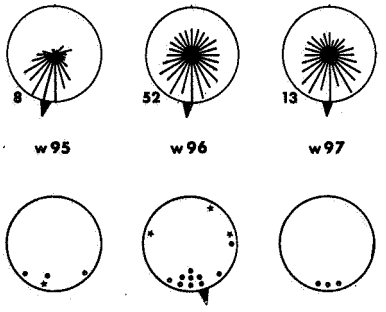

FIGURE 2. *Zugunruhe* orientation of immature birds allowed a 1-month exposure to natural surroundings (including celestial cues) just prior to the autumn migration season.

These early results suggested that some weak orientational ability did develop in some individual buntings without the need of any social contact with experienced birds or any prolonged visual-celestial experience during their early development. They further suggested that exposure to celestial cues resulted in considerably improved performances. Whether this was due to viewing the Sun, the stars, or, perhaps, integrating the two sources of information could not be determined.

A third group of buntings yielded data that are more difficult to interpret. They also were placed outdoors in a large aviary but

not until the migration season had begun (from September 15 until late October). These birds showed poor orientational abilities with only one of three individuals consistently directing its activity southward. The possible implications of these results will be discussed in a later section.

Experimental Series II

If a bunting must learn to recognize star patterns, those patterns will be useless as orientation cues unless their positions are learned with regard to some other directional reference system or marker.

In the summer of 1968 I again hand-raised indigo buntings for a series of experiments designed to retest the ability of "naive" birds to use celestial cues, and to determine the possible importance of celestial rotation in providing a reference axis for direction determination.

The first experimental group, group A, consisted of 10 birds that never left their windowless living quarters until I tested their orientational tendencies during the autumn migration season. The actual experiments were conducted under the artificial skies of Cornell's planetarium set to duplicate those present outdoors, with the exception that the experimental sky was held stationary. These birds never were allowed to view either the Sun or the natural night sky.

Each experiment lasted two hours and the hour-angle position of the planetarium sky was set to correspond with the mid-point of that two-hour period.

The results are shown in figure 3 and table 3. Of the 10 individual buntings, none demonstrated a clearcut directional tendency. This was true whether one analyzed the total activity of each bird or the distribution of mean directions from replicate tests. This contrasts strongly with previous results ob-

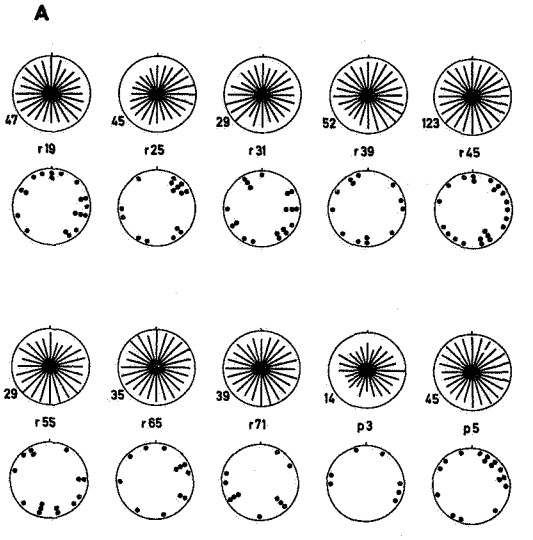

FIGURE 3. Orientation of young buntings prevented from viewing celestial cues during their early development and tested under a stationary planetarium sky.

tained from adult buntings which orient normally under stationary planetarium skies (ref. 9). Since the artificial sky contained the full complement of autumnal stars and star patterns (in their correct positions), the behavior of the young birds argues against a genetic recognition of specific stellar cues.

A second group of eight birds, group B, also was housed in a windowless room and prevented from obtaining any view of the natural sky. However, these individuals were taken into the Cornell planetarium and exposed to the artificial sky during the months of August and September. The artificial sky was set to duplicate that present outdoors and the star projector was modified to rotate at a speed of one revolution per 24 hours, thus duplicating the normal pattern of celestial rotation. The young birds continued to live in their indoor quarters, but, three times a week, I transferred them to the planetarium at 9 p.m. and returned them to their indoor cages

TABLE 3.—*Orientation of Young Indigo Buntings Prevented from Viewing Celestial Cues During Their Early Development and Tested Under a Stationary Planetarium Sky*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r19		963	0.878	0.649	.....
	19		0.261	0.836	.....
r25		846	0.144	0.392	.....
	15		0.393	0.616	.....
r31		573	0.942	0.388	.....
	19		0.539	0.261	.....
r39		1086	0.522	0.563	.....
	13		0.942	0.422	.....
r45		2706	0.497	0.147	.....
	22		0.449	0.356	.....
r55		604	0.528	0.131	.....
	15		0.449	0.102	.....
r65		762	0.861	0.701	.....
	12		0.530	0.751	.....
r71		722	0.811	0.270	.....
	11		0.316	0.069	(195)
p3		238	0.692	0.500	.....
	7		0.067	0.907	.....
p5		964	0.644	0.695	.....
	16		0.111	0.943	.....

between 4:30 and 5 a.m. (Eastern Daylight Time).

During the migration season, these birds were tested under the identical, stationary, planetarium sky described for group A. In fact, birds from both group A and group B usually were tested simultaneously in the planetarium.

The rationale for testing birds under a stationary sky, thereby denying them direct access to rotational information, was to test whether they had integrated information from celestial configurations with the potential reference framework provided by the axis of rotation. The experimental design called for retesting these birds under a moving sky if orientational tendencies failed to appear with stationary sky conditions.

Figure 4 and table 4 show that such an integration apparently did take place. Exposure to stellar cues, including celestial motion, resulted in greatly improved orientation. Of the eight birds, seven exhibited southerly preferences in both total activity and nightly mean headings. In keeping with previous reports, the behavior of immatures was less accurate than that of adults tested under similar conditions (refs. 10, 14, and personal communication from W. J. Hamilton, III), but the directional tendencies were highly

significant and all lay between SSE and SSW, well within the normal migratory range for the species.

A third group of buntings, group C, also was exposed to planetarium skies prior to the migration season. After becoming self-sufficient, these birds were taken on three different nights each week and exposed for a similar length of time to an artificial sky. However, this sky was abnormal in several respects.

Once again, I had modified the star projector, this time by constructing a special attachment arm that allowed the celestial sphere to be rotated about any axis of my choosing. For group C, I selected the bright star Betelgeuse as the new "pole star" and the constellation Orion became the dominant pattern in the new "circumpolar" area of the sky. The speed of rotation (15° per hr) and the direction (clockwise) remained as they were before.

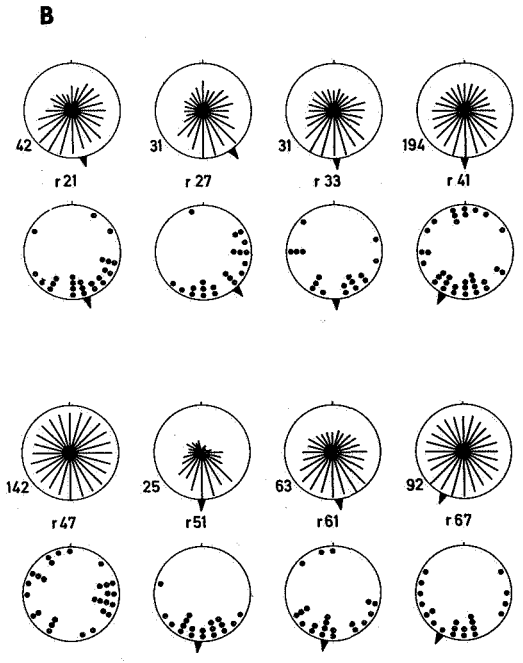

FIGURE 4. Orientation of young buntings permitted regular viewings of a normal, rotating planetarium sky during their early development and tested under a stationary artificial sky.

I selected this new sky setting for several reasons. First, a bright star was located at the pole of the new axis. Second, a very bright constellation was located in the "circumpolar" area, an area shown to be of importance in the celestial orientation process of indigo buntings (ref. 9). Third, the "hour angle" position was selected carefully so that the actual northern circumpolar stars (in particular the constellations Ursa Major and Cassiopeia and the star Polaris) were present in this artificial sky. They were located just to the south of the new "celestial equator" and moved progressively across the sky from east to west as the night progressed.

If celestial rotation provides a reference axis for the use of stellar cues, then the birds of group C might adopt this incorrect axis and orient their migratory activity in an inappropriate direction. On the other hand, if young birds possess a genetically predetermined star map as has been proposed by some authors (ref. 1), then the birds should orient "south" with reference to the normal circumpolar area of the sky. These two "south" directions should be easily distinguishable since they range from 110° to 180° apart in these incorrect planetarium settings.

Figure 5 and table 5 give the results from these birds when plotted relative to true stellar north—with Polaris dictating the northward direction. Of the seven birds, only two showed significant directional tendencies (measured by either the Rayleigh or the "*V*" test): r23 preferred a northwesterly bearing while r57 aimed southward. The accumulation of mean bearings for r57 did not deviate from random. Neither did the orientation behavior of the remaining five individual birds.

Compare these results with figure 6 and

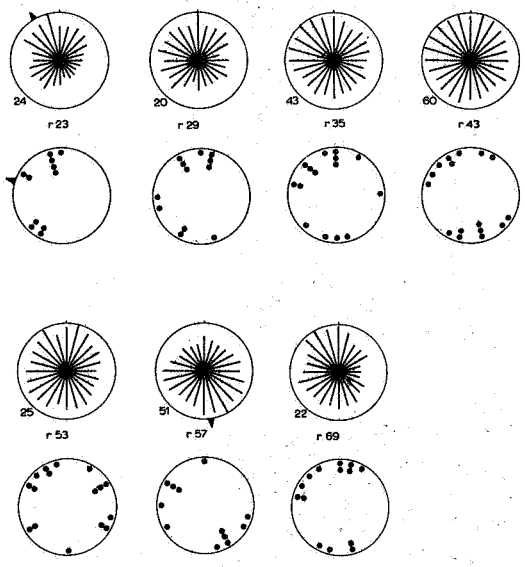

FIGURE 5. Orientation of young buntings exposed to a planetarium sky that rotated at 15° per hour about an incorrect axis during their early development. Data are plotted with reference to true stellar north (position of Polaris dictating north).

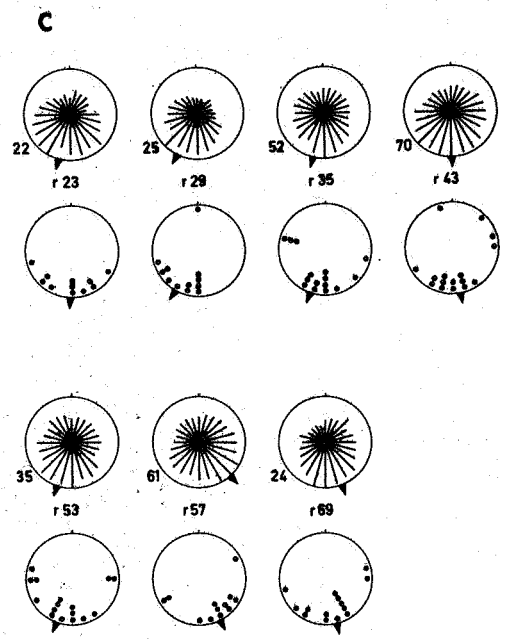

FIGURE 6. Same data as in figure 5 but plotted with new "pole star" (Betelgeuse, of the constellation Orion) designating "north" or 0°.

table 6 in which the data from group C are replotted relative to the new axis of rotation —with the position of Betelgeuse defining north. All seven birds now display a "southerly" orientation indicating a realignment of directional behavior to correspond with the new axis of rotation. The mean bearings range from 138° to 211° and the values obtained from total activity measures and distribution of nightly means are in very close agreement.

Once again these results are inconsistent with the hypothesis of a predetermined template of star positions. Rather they imply an important role of celestial rotation in the maturation of migratory orientation abilities.

Experimental Series III

Previous work has suggested that many individual adult indigo buntings rely for direction determination upon star patterns located near the northern axis of rotation (ref. 9). I was curious to learn whether this was also true for immatures. In particular, might the birds of group C have come to rely upon "wrong" star patterns situated near the artificial axis of rotation?

I tested this by removing selected stellar information from the planetarium sky by attaching a cardboard mold over the appropriate portion of the star projector. As in experimental series II, all observations were made under stationary skies.

I presented birds from group B with a planetarium sky in which the northern circumpolar area, defined as encompassing an area within 35° of Polaris, had been blocked. The results (fig. 7 and table 7) indicate a

TABLE 4.—*Orientation of Young Buntings Permitted Regular Viewings of a Normal, Rotating Planetarium Sky During Their Early Development and Tested Under a Stationary Artificial Sky*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r21		684	0.002	0.000	169°
	24		0.000	0.000	165°
r27		455	0.009	0.006	145°
	21		0.001	0.003	138°
r33		487	0.004	0.000	178°
	17		0.005	0.001	182°
r41		3293	0.000	0.000	182°
	32		0.079	0.024	208°
r47		2932	0.440	0.205	.....
	28		0.718	0.452	.....
r51		251	0.000	0.000	181°
	19		0.000	0.000	186°
r61		1024	0.000	0.000	174°
	21		0.003	0.001	191°
r67		1777	0.088	0.025	207°
	21		0.001	0.001	195°

high degree of individual variability. Of six active birds, only two continued to display southerly tendencies, r33 to the south, and r27 to the southeast. One additional bird, r41, took up a new and inappropriate orientation to the northeast. The behavior of the three remaining birds failed to deviate from random.

These results are consistent with previous findings from adults: Blocking the northern sky adversely affects the orientation of most buntings.

I subjected the birds of group C to two sets of blocking experiments. First, I removed all the stars located in the southern celestial hemisphere. Since the true northern circumpolar stars were located just south of the celestial equator in the C sky, this manipulation eliminated them as potential cues.

The results of six birds tested under these conditions are shown in figure 8 and table 8. Again, inter-individual variation is high; but four individual buntings continued to orient southward.

This contrasts with the results obtained from the same birds when I removed the *new* "circumpolar stars" (within 35° of Betelgeuse) from the sky. Figure 9 and table 9 reveal that all birds of group C failed to show significant directional preferences under

TABLE 5.—*Orientation of Immature Buntings of Group C Plotted With Reference to True Stellar North (Position of Polaris Dictating North Point)*[a]

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r23		354	0.04	0.99	328°
	11		0.03	0.86	294°
r29		343	0.25	0.91	.....
	12		0.09	0.94	(314°)
r35		813	0.15	0.92	.....
	15		0.13	0.91	.....
r43		1249	0.20	0.90	.....
	16		0.88	0.38	.....
r53		592	0.66	0.69	.....
	16		0.34	0.93	.....
r57		1056	0.20	0.03	173°
	12		0.59	0.17	.....
r69		379	0.26	0.75	.....
	14		0.14	0.93	.....

[a] The eighth bird in this group, r49, developed the habit of "somersaulting" in the orientation cage. Since the resulting ink smudges represented an aberrant behavior pattern, they are not treated in this analysis.

this condition. I only performed two replicate tests under these skies, so the sample sizes of mean directions are insufficient for statistical analyses. However, a qualitative glance shows that a clumping of means occurred for only one bird, r43, and that clumping was in an inappropriate direction. Although Betelgeuse and the constellation Orion were absent in this experimental sky, the true northern circumpolar stars were present. The fact that the buntings were unable to orient implies that these patterns provided insufficient information for direction determination.

The most important area of the night sky thus appears to be defined not by the presence of specific stellar configurations but by a relationship to the axis of celestial rotation.

Experimental Series IV

Many studies of behavioral development have stressed the importance of sensitive or critical periods during which the young animal responds preferentially to certain types of sensory input. In the case of bunting orientation, might such a developmental phase exist prior to the first migration season? Or would a prolonged exposure to celestial cues following the autumn migration period enable birds of group C to re-adopt the normal migration direction in future years?

Following the experiments in the autumn of 1968, I placed the birds from group C in a large, windowless, indoor aviary, 2.4 × 3.7 meters. Photoperiod was maintained by an

TABLE 6.—*The Data of Table 5 Re-analyzed With the New "Pole Star" (Betelgeuse of the Constellation Orion) Designating "North" or 0°*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh (test)	p (V test)	Mean direction
r23		354	0.017	0.003	195°
	11		0.001	0.000	186°
r29		343	0.001	0.000	207°
	12		0.001	0.001	211°
r35		813	0.015	0.002	194°
	15		0.001	0.000	198°
r43		1249	0.000	0.000	180°
	16		0.006	0.001	172°
r53		592	0.063	0.014	200°
	16		0.001	0.001	201°
r57		1056	0.002	0.005	138°
	12		0.003	0.002	156°
r69		379	0.013	0.003	161°
	14		0.001	0.009	600°

astronomical time-clock set for 18° north latitude. This served to simulate the changes in daylength typical for the wintering grounds of this species. In the spring, I moved these birds outdoors to an aviary, 2.4 × 4.9 meters, providing a full view of natural surroundings and celestial cues (including celestial motion). The birds lived at this outdoor location from early May until the end of autumn migration season in early November 1969.

Six of the original birds molted normally, deposited large quantities of fat, and exhibited nocturnal activity. After six full months of access to normal visual-celestial information, I returned these birds to the planetarium and tested them under the incorrect, stationary skies they had been exposed to a year previously. This sky was selected to present the birds with a choice of southern migration directions. The star Betelgeuse was located at an altitude of 42° in one direction; the pole star, Polaris, was situated at a comparable altitude in a different direction. Neither pole star coincided with the direction of either geographic or magnetic north. (Considering Betelgeuse as 0°, geographic north is 48° and magnetic north, 38°.) I tested the birds only once each night, always at the same sky setting. This prevented them from obtaining indirect information about the axis of rotation by comparing the movement of stars located at different points in the celestial sphere between successive sky settings.

The orientation performances of these birds are shown in figure 10 and table 10. Although the sample sizes are rather small for some birds, five of the six individuals show a clear tendency to orient south relative

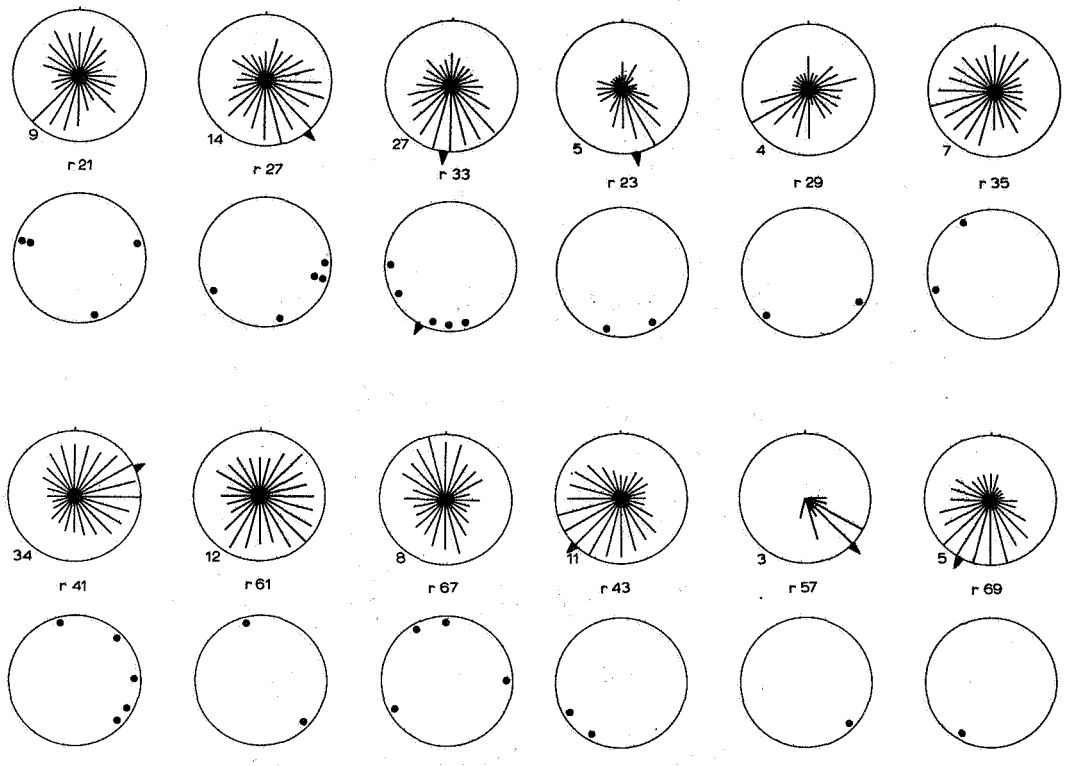

FIGURE 7. Orientation of immature buntings of group B under a planetarium sky in which the circumpolar stars have been removed.

FIGURE 8. Orientation of buntings of group C under a planetarium sky in which the southern stars have been blocked.

to the *incorrect* axis of rotation. The birds not only took up directions remarkably similar to those selected the previous year, they also showed a decrease in the amount of scatter in their nocturnal activity.

This implies that the birds had not adjusted to a new axis of rotation; they had not relearned the positions of star patterns relative to a new reference framework. Rather, the results are consistent with the hypothesis of a sensitive period in the development of indigo buntings, a period during which the young are highly receptive to rotational input. During later life buntings show a lesser tendency to modify their behavior as a result of visual-celestial experience.

The poor orientational results of the buntings in group C in experimental series I are of interest in this regard. These birds were placed outdoors and allowed visual exposure to celestial cues after the initiation of the migration season. Yet they failed to show the improvement in orientational ability attained by individuals of a second group given similar exposure prior to the time of migration (figure 2). Therefore the optimal period for learning stellar cues might coincide with the period of pre-migratory development. Stated another way, might this sensitivity decrease with the onset of actual migratory behavior? Answers to these questions must await future experiments employing larger samples of birds.

TABLE 7.—*Orientation of Immature Buntings—Group B—Under a Planetarium Sky in Which the Circumpolar Stars Have Been Removed*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh (test)	p (V test)	Mean direction
r21		134	0.93	0.39	.....
	4	insufficient sample size.....		.....	
r27		223	0.06	0.03	142°
	5		0.17	0.08	(135°)
r33		394	0.00	0.00	186°
	5		0.03	0.01	205°
r41		552	0.00	0.93	66°
	5		0.14	0.65	.....
r61		211	0.46	0.24	.....
	2	insufficient sample size.....		.....	
r67		124	0.74	0.72	.....
	4	insufficient sample size.....		.....	

TABLE 8.—*Orientation of Immature Buntings—Group C—Under a Planetarium Sky in Which the Southern Stars Are Missing*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r23		47	0.26	0.05	170°
	2	insufficient sample size.....		.....	
r29		46	0.65	0.17	.....
	2	insufficient sample size.....		.....	
r35		112	0.52	0.38	.....
	2	insufficient sample size.....		.....	
r43		176	0.03	0.04	227°
	2	insufficient sample size.....		.....	
r57		12	0.05	0.04	136°
	1	insufficient sample size.....		.....	
r69		71	0.09	0.02	206°
	1	insufficient sample size.....		.....	

TABLE 9.—*Orientation of Immature Buntings—Group C—Under a Planetarium Sky in Which the "Circumpolar" Stars (Within 35° of Betelgeuse) Have Been Blocked*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r23	1	44	0.88	0.69	.....
		insufficient sample size.....	.....		
r29	2	63	0.88	0.59	.....
		.....	.....	.....	
r35	2	167	0.58	0.18	.....
		.....	.....	.....	
r43	2	257	0.72	0.79	.....
		.....	.....	.....	
r53	2	90	0.95	0.38	.....
		.....	.....	.....	.....
r57	2	171	0.34	0.93	.....
		.....	.....	.....	
r69	2	167	0.44	0.36	.....
		.....	.....	.....	

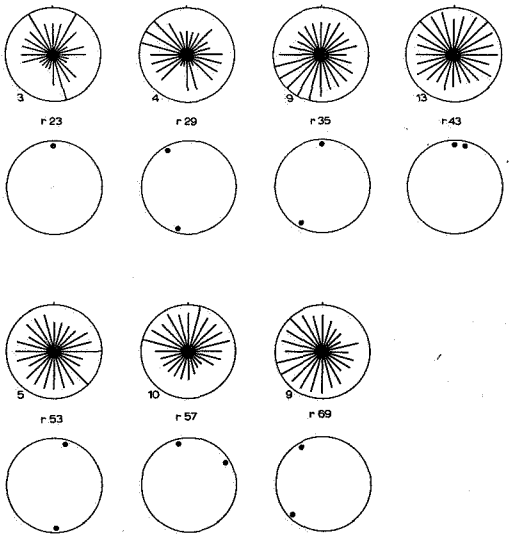

FIGURE 9. Orientation of buntings of group C under a planetarium sky in which the "circumpolar" stars (within 35° of Betelgeuse) have been blocked.

DISCUSSION OF EXPERIMENTS

These series of experiments furnish strong evidence that early visual experience plays an important role in the maturation of celestial orientation abilities in indigo buntings. In the hopes of stimulating both discussion and future experimentation, I offer the following working hypothesis. I propose that young buntings have a predisposition to respond to the apparent rotational motion of the night sky. This responsiveness is not dependent upon prior migratory experience; neither is it rewarded in the conventional sense of the term. The experiments in series IV suggest that the peak in responsiveness to rotational information is present during the first summer of life, prior to the first migration season.

The fact that stars located near the celestial axis move through much smaller arcs (have slower linear velocities) than those near the celestial equator could allow the

TABLE 10.—*Orientation of Indigo Buntings of Group C in the Autumn of 1969, Following One Full Summer of Exposure to Natural Surroundings and Celestial Cues*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r23		54	0.00	0.00	181°
	4	insufficient sample size			
r29		134	0.00	0.00	223°
	5		0.28	0.09	(218°)
r43		391	0.88	0.32	.....
			0.92	0.34	.....
r53		214	0.01	0.00	190°
	6		0.03	0.01	191°
r57		234	0.01	0.00	150°
	6		0.21	0.04	160°
r69		28	0.03	0.01	183°
	2	insufficient sample size			

birds to locate a north-south directional axis. Stars and patterns of stars are of no value for direction finding until their positions are learned relative to some reference location. If the birds come to associate certain patterns of stars with areas of either fast or slow rotation, the axis of motion can become one such reference system. The results from experimental series III suggest that young buntings tend to concentrate their attention on areas of slow rotation, thereby coming to rely upon the circumpolar sky areas. Within this broad constraint, individual birds could learn a variety of star groupings. Such a hypothesis is consistent with the high degree of individual variability obtained in blocking experiments with adult buntings. This redundancy in pattern recognition could be highly adaptive since clouds frequently obscure portions of the sky from view. A preferential reliance upon circumpolar sky areas further assures the presence of familiar star groupings at all seasons and times of night since such cues are rarely below the horizon at the northern latitudes through which indigo buntings migrate.

Once an integration of stellar and rotational information has occurred, a bird should be able to locate the rotational axis (and, hence, a reference direction) from the geometry of star configurations alone. This implies that celestial motion *per se* need not be an important cue for adult birds. In point of fact, the accurate orientation of several species of caged migrants under stationary planetarium skies (refs. 1, 15, unpublished observations by S. T. Emlen, and personal communication from S. A. Gauthreaux, Jr.) demonstrates that such motion is not essential for direction determination. But lack of essentiality need not imply that rotational cues cannot be used as a source of directional information. Two of four birds in group A of experimental series I showed southerly biases when tested under the natural night sky although I had prevented them from viewing the sky during their early development. These results differed from those obtained

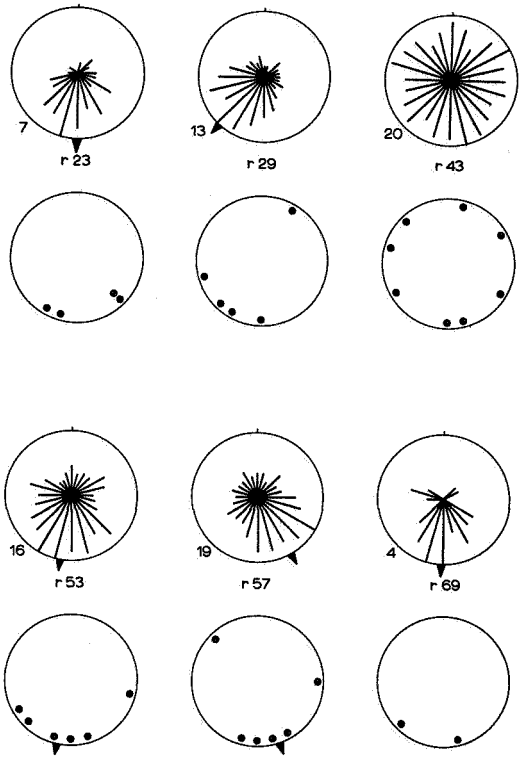

FIGURE 10. Orientation of buntings of group C in the autumn of 1969 following a summer of exposure to natural surroundings and celestial cues.

from birds kept in similar visual isolation but tested under a stationary starry sky (group C, experimental series II). It is conceivable that the former birds integrated pattern information with the visible rotation during the first few hours of exposure to the natural night sky; or, the two buntings might have used rotational information directly as an orientation cue. (This hypothesis need not imply that buntings directly perceive the slow rate of celestial motion. One could locate the axis of rotation by making observations over longer periods of time and comparing the degree of movement of stars located at different points in the celestial sphere.)

All of this speculation avoids the question of why the young migrant orients southward on its first flight. Rotation, in this hypothesis, merely provides a stable reference axis. The use of this reference to select a southerly heading as opposed to any other remains a topic for future investigation.

This paper has concentrated on only one aspect of the migratory orientation problem, the use of stellar cues. Future experiments should consider the possible integration of other types of directional information into adult guidance systems. For example, we know that most nocturnal migrants are daytime animals except during the migration season, and experiments by St. Paul (ref. 16) and Shumakov (ref. 17 and 18) show that several such species possess an ability to orient by the Sun. The integration of stellar information with information about the path of the Sun and, in particular, the position of sunset might lead to a more accurate orientation ability. A possible selective advantage for such a system is easy to imagine for birds that migrate over large bodies of water and might be unable to land with the coming of sunrise.

Similar arguments could be made for the coupling of celestial information with other types of guidance cues, be they topographic, magnetic, or meteorological.

Finally, one might inquire about the possible selective advantage of a maturation process that integrates experience-dependent and experience-independent factors and rotational and configurational information. One possible explanation lies in the long-term unreliability of stellar cues themselves. Agron (pp. 525–526 of ref. 19) has noted that the positions of stars are not constant through evolutionary time. This is due, primarily, to the precession of the Earth's axis. Agron likened this to the wobbling of a spinning top and states:

The angle of tilt of the Earth's axis remains constant, but the direction of the axis changes. In a period of 25,800 years, the gyrations, in a cone, of the earth's axis cause the celestial pole to make one circuit about a circle of 23.5° radius.

This motion produces marked seasonal and latitudinal changes in the apparent positions of stars, the "spring" stars of the present becoming "autumn" stars in 13 000 years, and vice versa. The values of declination also change; as the axis moves through its circle of 47°, Vega becomes the new pole star and the declination of Polaris shifts from 90° north to 43° north. Similar changes occur for all stars with the result that the stellar information typical for any given latitude or season is altered markedly.

The implications of these changes for the evolution of celestial navigation are obvious. If migrants are to rely on a genetically fixed star map that they have inherited, the rate of genetic change must be rapid enough to allow for these changes in celestial position.

A maturation process involving the coupling of stellar information with a secondary set of reference cues would minimize this problem. The axis of apparent celestial rotation is well suited to function as one such cue because this axis is aligned with geographic north-south regardless of what particular stars are located at its "poles."

Over a decade has passed since Lehrman (ref. 20) issued his warning to ethologists that simple categorization of behaviors as "innate" could serve to discourage research on behavioral development. The lack of data on the maturation of guidance mechanisms bears witness to the truth of his statement. Hopefully this paper will provide a small stimulus to others to initiate studies in this area, for I feel that such investigations may lead to new discoveries concerning the functioning of animal orientation systems.

APPENDIX 1

Age and Sex Data for Hand-Raised Birds Used in Experimental Series I

Bird	Sex	Age at capture	Fledging date	Group	Eyes at capture
w88	M	8 days	21 June	A	open
w89	F	10 days	30 June	A	open
w90	F	9 days	26 July	C	open
w91	F	8 days	27 July	C	open
w92	M	8 days	27 July	C	open
w93	M	3 days	8 August	A	closed
w94	F	3 days	8 August	A	closed
w95	F	4 days	8 July	B	closed
w96	F	4 days	8 July	B	closed
w97	F	3 days	30 June	B	closed

APPENDIX 2

Age and Sex Data for Hand-Raised Birds Used in Experiment Series II, III and IV

Bird	Sex	Age at capture	Fledging date	Group	Eyes at capture
r19	F	5 days	June 30	A	slits
r21	F	9 days	June 21	B	open
r23	M	9 days	June 21	C	open
r25	M	4 days	July 11	A	closed
r27	M	4 days	July 11	B	closed
r29	M	4 days	July 11	C	closed
r31	M	4 days	July 11	A	closed
r33	M	5 days	July 10	B	slits
r35	F	5 days	July 10	C	slits
r39	F	8 days	June 30	A	open
r41	F	8 days	June 30	B	open
r43	F	8 days	June 30	C	open
r45	M	8 days	June 30	A	open
r47	M	9 days	July 18	B	open
r49	F	9 days	July 18	C	open
r51	F	4 days	July 22	B	closed
r53	M	4 days	July 22	C	closed
r55	F	4 days	July 22	A	closed
r57	M	9 days	July 23	A	open
r61	F	9 days	July 23	B	open
r65	F	8 days	July 23	A	open
r67	F	8 days	July 23	B	open
r69	F	9 days	July 29	C	open
r71	M	6 days	July 27	A	open
p3	F	5 days	August 3	A	slits
p5	F	5 days	August 3	A	slits

DISCUSSION

QUESTION: Do you know of any data that suggest that motion, *per se*, in celestial bodies is a cue? Can birds see the movement of Sun, Moon, or stars directly?

EMLEN: That is a good question. However, I have no new information that pertains directly to it. In order to use celestial motion as I am suggesting, one need not perceive it directly. One easily can locate the axis of rotation by making observations over long periods of time and comparing the degree of movement of stars located at different points in the sky. Whether celestial motion itself is actually visible is a debated subject. Horridge has concluded that some crabs can detect movements well below the rate of celestial rotation. For birds, however, this remains an unresolved question.

QUESTION: The data for group C are plotted in two ways. How can one be oriented and the other not?

EMLEN: Experiments were performed twice a

night. A typical experiment lasted two hours and the hour-angle position was set for the mid-point of that two-hour period. Consequently, the birds of group C oriented under two different skies each night. Since the times of the experiments also varied somewhat, this resulted in the accumulation of oriented responses under a variety of hour-angle settings. The position of the "pole" star, Betelgeuse, did not change during these sky shifts, but the position of the real north star, Polaris, did. If the birds were orienting relative to a "Betelgeuse axis," then plotting the data relative to Polaris would be equivalent to rotating each data distribution by an amount equal to the difference in azimuth positions of Polaris and Betelgeuse. This difference is not constant but changes with changes in hour-angle settings, so an increase in scatter results.

QUESTION: Where is magnetic north in the Cornell planetarium?

EMLEN: This is variable since the experimenter can orient the star projector to make stellar north correspond to any direction of his choosing. To guard against a misinterpretation of planetarium results, various types of controls are imperative. One of these involves testing birds under a starless dome, or placing a sheet of frosted glass over the top of an individual orientation cage to simulate "instant overcast." Another control is to change the north point and then note whether the birds change their behavior in keeping with the artificial sky. In experimental series II, the birds of groups A and B were subjected to both control procedures. Depending upon the sky setting, magnetic north was located at either 130° or 310°. True geographic north would be at 140° and 320°. With the star projector modified to rotate abnormally for group C, the control of reversing the north point became impractical. For these birds magnetic north was 40°, true geographic north 50° (considering Betelgeuse as 0°).

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An Approach Toward an Analysis of the Pattern Recognition Involved in the Stellar Orientation of Birds

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AT PRESENT, there seems to be no reason to doubt that birds make use of the stars as orientational cues during their nocturnal migrations (refs. 1 and 2). Probably the stars are not the only orientational cues (refs. 3 to 5), but we will not be concerned with the problem of other parameters here. Instead, we will deal with the mechanism of pattern recognition as a requirement of stellar orientation. Before it is possible to analyze it in detail, however, it is necessary to obtain a general view of the capabilities of the birds. As yet, not much more has been achieved.

The experimental method of the analysis was described earlier in detail (refs. 6 and 7); thus, a short outline may suffice. A bird is attached to a turntable with its head in the center. Its visual field is limited by a black cylinder shielding the horizon and lower parts of the sky, normally up to 40°. The turntable rotates with a speed varying between about 1 and 4 minutes per cycle. A conditioning stimulus consisting of a weak electrical shock is applied whenever the bird's axis points in a certain direction. After a period of training, an increase in heart rate anticipating the shock can be recorded, provided that the stimulus situation enables the bird to recognize the direction at which the shock is given. Accordingly, in critical tests without any shock, we get a maximum frequency of heart beats whenever the animal is passing the training direction. An electronic system controls the experiment automatically, and the data are recorded on paper tape and analyzed by a computer.

Figure 1 illustrates the kinds of data yielded by this technique. It shows three procedural steps of the analysis of 60 test cycles without shock. In part A, the original curves of heart rate are plotted with frequency (beats/sec) as the ordinate. Clearly there is a general maximum in the training direction, but the field covered by the individual curves is rather large. This results mainly from the variability in the basic heart rate and in absolute amplitude of the training responses at different times. Compensation for these variables results in normalized curves (B) with relative units at the ordinate,

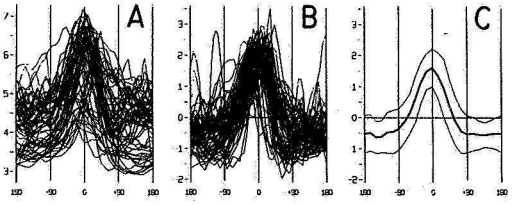

FIGURE 1. Heart rates of European teal (*Anas crecca*) during 60 test cycles without shock under the condition to which it had been trained (30 cycles clockwise and 30 counterclockwise). 0° at abscissa stands for training direction. (A) Original curves with frequency of heartbeats per sec as the ordinate. (B) Same data after normalization. This was done by calculating mean level and standard deviation for each individual cycle. Deviation of each point from the mean level was determined and divided by standard deviation. Zero stands for mean value of all individual curves. (C) Mean curve ± standard deviation derived from part B.

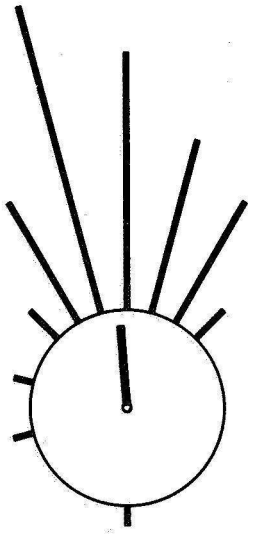

FIGURE 2. Frequency distribution of the maxima of 60 curves shown in figure 1. Training direction points upwards. Smallest length of a line refers to one maximum. Mean vector calculated from this distribution is drawn in the center. Radius of the circle coincides with greatest possible length of this vector, i.e., $a = r = 1$. (These are the basic data of the tests summarized in figure 9A.)

zero being the mean heart rate per cycle. The result of this procedure is a concentration of the curves, and the training effect becomes clearer. Part C shows the mean curves and standard deviations derived from part B.

Another much simpler kind of analysis of the same data is shown in figure 2. In this case, the direction of the maximum in each cycle is determined, and the diagram shows the frequency distribution of these 60 directions. From this distribution a mean vector can be calculated, the direction and length of which summarize conveniently the result of a particular experiment.

It has been shown that the orientational cues are picked up visually either from the natural night sky or from an artificial sphere in a planetarium (refs. 6 and 7). Besides corroborating this fact, the experiments presented here concern the effect of manipulation of the projected star patterns on the orientational responses of birds.

RESULTS

Simulated Natural Patterns

The following series of experiments with a mallard (*Anas platyrhynchos*) were conducted under a planetarium sphere simulating the natural starry sky at the same longitude during the respective time of day and season. Latitude was adjusted to 40° north, while the real place was at 48°. The lower parts of the sky up to the height of Polaris were blocked from view by the shielding cylinder. The results are shown in figure 3.

In series I, beginning in June, the bird was trained for 6 hr in the first part of the night. During these 6 hours the projected sphere rotated from hour angle of Aries 210° to 300°. At irregular intervals varying between about 15 min and 2 hr, the training program was interrupted, and a critical test

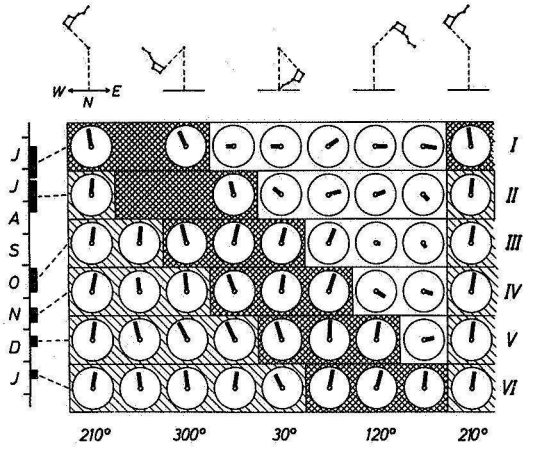

FIGURE 3. Mallard R, tests under simulated natural skies adjusted to 8 hour angles of Aries with 45° (= 3 hr) intervals. Respective position of Ursa Major together with Polaris is shown for illustration. During each of the series I to VI (time scale at the left: June to Jan.), bird was trained within interval indicated by cross-hatchings under a sphere continuously rotating from the respective left-hand to right-hand position. Parallel hatchings indicate former training conditions, while no hatching stands for conditions not yet used for training. Mean vectors are shown, as explained in figure 2, the training direction (west) pointing upwards. Sample size for each diagram varied between 40 and 80 test cycles.

was inserted. Normally it consisted of 10 cycles, five clockwise and five counterclockwise. These tests were made at one of eight positions of the sky around the total 360° of hour angles. In series II, the 6 hour training period was shifted 45° or 3 hours clockwise, and so on to series VI conducted in January, when the circle was closed; i.e., all test positions were covered by training.

Within the respective training phase (in fig. 3 marked by cross-hatchings), the maxima of heart rate were concentrated around the training direction. At the right of this phase, i.e., under skies not yet used for training, the bird appeared disoriented or ill-directed. However, under skies formerly used for training at the left, it responded as well as under the current training patterns.

Before the experiments, this adult mallard was living under open air conditions. Thus, it has had the opportunity to observe the night sky. It was not a matter of course, therefore, that it did not correctly respond under stellar patterns not yet used for training. There are at least two possibilities why it did not. Either the bird did not identify the planetarium sky with the natural starry sky, or it merely failed to transpose the compass direction at which the shock was applied, from the training condition to the test condition where it had never been shocked so far.

More remarkable than this negative result may be the positive one. Once trained under a certain segment of the stellar sphere, the bird kept in mind the respective configurations while learning additional patterns. At the end of the experiments, this mallard mastered all meridian positions at latitude 40° N. In series VI, the time between training and testing at hour angle of Aries 210° was about half a year.

As a byproduct of these series, we are led to the conclusion that the circadian clock is not involved in this kind of orientation. During training, the stellar sphere was always in phase with the bird's clock, but during testing it was out of phase up to 12 hr back and forth. Provided that the bird was already familiar with the respective patterns, it never deviated from its normal direction of response (ref. 8). This is in accordance with the findings of Matthews (ref. 9) and Emlen (ref. 10). It seems doubtful, however, whether the stellar orientation is generally independent from time (or longitudinal) shifts because there are other findings suggesting that time relations might be taken into account either in certain species or (and) under certain circumstances (refs. 1 and 11

to 14). But this is not a question to be discussed here, for it involves not only the determination of a specific compass direction but also the choice of the desired direction itself during actual migration.

Artificial Patterns

Is directional training only possible under natural or simulated natural skies? Or is it possible under any arbitrary "starry sky" too? With the planetarium projector we are using (shown in ref. 7), it is easy to produce distributions of stellar patterns never and nowhere occurring in nature. For this purpose, the 31 single projectors composing the whole sphere were interchanged. Thus, the interrelations between the stars within an individual projector field remained constant, but the fields were mixed up, and all stars were dislocated with respect to the celestial coordinates.

It has been shown earlier that training under such conditions is indeed possible (ref. 7). However, at that time the question still remained open whether there might be a gradual difference between the performances under a simulated natural sky and under a totally artificial sky. Because of the interindividual variability of training performances, the same individuals had to be used under both conditions. Figure 4 shows, in a mallard as well as in a European teal (*Anas crecca*), that there are no marked differences between the orientational responses under both kinds of starry skies.

Mode of Learning and Mistaking

How do the birds learn, and what do they learn? This question is far from being solved, and the experiments to be described now can just show one of the starting points for further analysis.

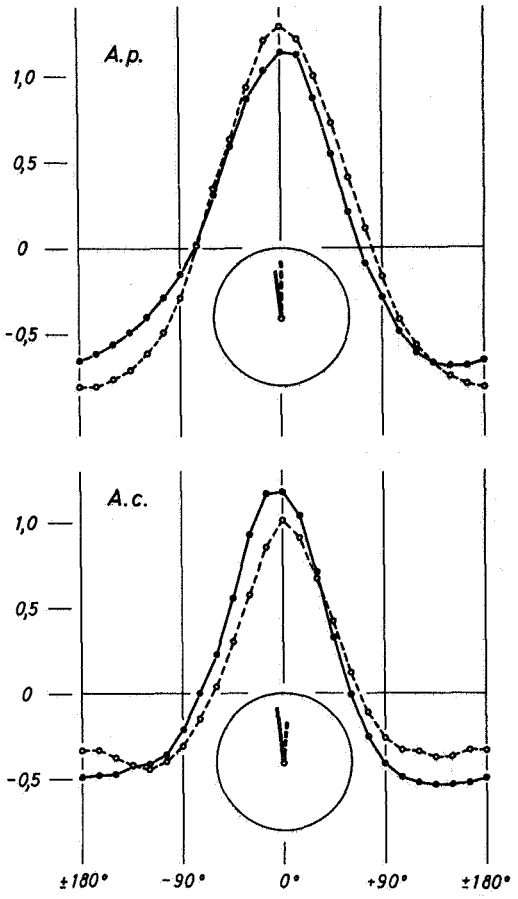

FIGURE 4. Mallard Q (top) and teal A (bottom), mean heart rates and mean directions of the maxima under simulated natural skies (solid lines) and under artificial skies (broken lines). Curves are derived as in figure 1C, and the vectors as in figure 2. Each curve and each vector, respectively, represents 320 test cycles with several adjustments of the projector. (These are overall means of the parts marked by crosshatchings in figures 7 and 8, series I, II, and IV, plus 40 cycles in series IV with the sphere actually moving.)

Figure 5 contains the most interesting parts of a series of tests made with a teal. Two meridian positions of the simulated natural sky are involved, hour angles 60° apart from each other. In series I, the bird was

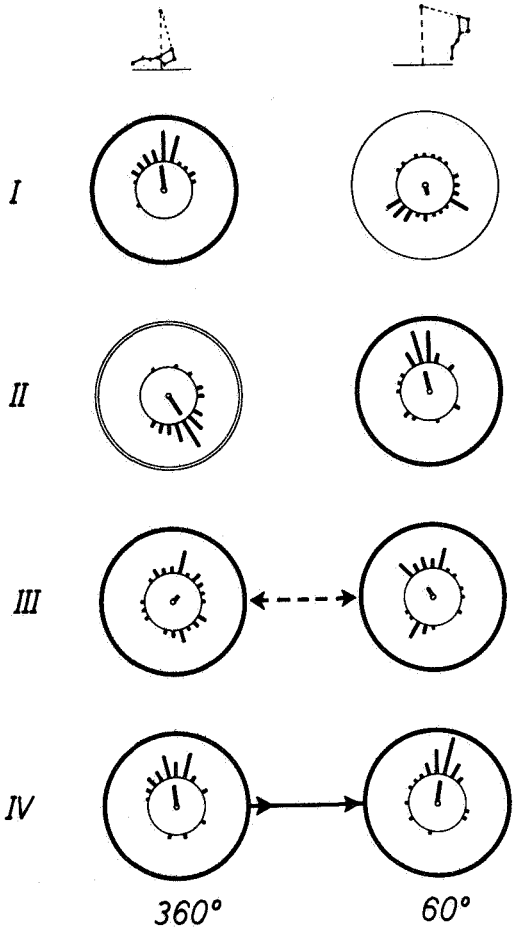

FIGURE 5. Teal A, distributions of the maxima of heart rate and mean vectors derived from them, under two meridian positions of the sphere at simulated latitude 40° N. Training direction (upwards) equals north. Each diagram is based on 40 test cycles. In series I to IV different conditions for training were used.

trained under a motionless starry sky in the first position. The result was as expected; i.e., good orientation with the sky in training position, disorientation under a sky not yet used for training. Thereafter (II) the bird was trained under the other position to the same direction (north). Now it was correctly oriented at 60°, but contrary to my expectation, it had lost its correct orientation under the former training condition at 360°. Nevertheless, it showed an obviously oriented reaction here also, but the maximum heart rate appeared in nearly the opposite direction. Apparently the bird tried to identify the two patterns with each other, and it succeeded at best by identifying the SSE direction under the previous training pattern with North under the current training pattern. The respective planetarium skies are shown in figure 6 in an orientation in which their essential parts obviously looked similar for the bird. For the reader the similarity may not be obvious, nor is it for the writer, but it will be shown below that a mallard reacted in exactly the same way.

During series III the bird was trained alternately under both patterns in intervals of about 30 to 60 min. A bimodal distribution of the responses resulted now, suggesting a conflict situation for the bird. However, the problem was solved by training the teal under a sky continuously moving from the first position to the second one in the natural duration of 4 hr (series IV). Now, after being exposed to all the transitional stages, the bird was able to recognize the training direction under both patterns.

Actually during these experiments the teal was not only tested under positions 360° and 60° as shown in figure 5, but also at intervals of 15° between hour angles 330° and 90°. The complete series is shown in figure 7, together with the reactions of a mallard under the same conditions. The results from these two individuals belonging to different species are remarkably similar, which suggests that both birds evaluated the stellar patterns in a similar manner.

The same two birds also reacted quite similarly in an analogous series under artificial skies not simulating any conditions out-

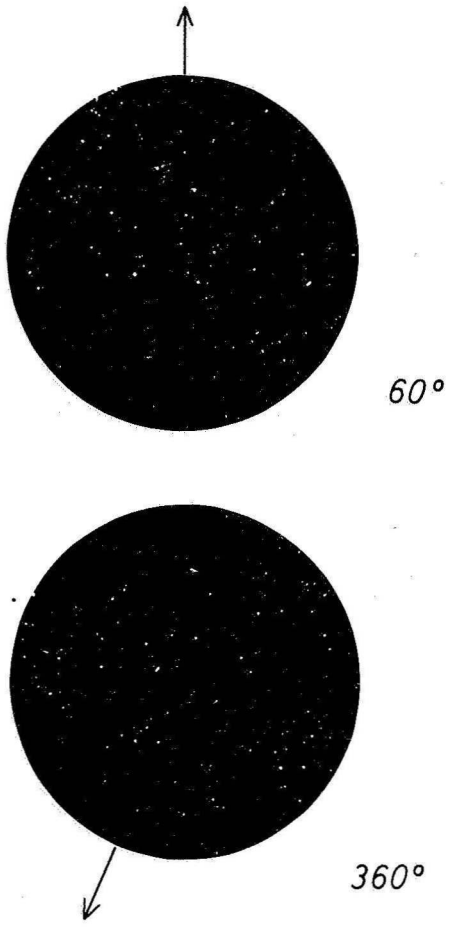

FIGURE 6. Planetarium skies adjusted to hour angles of Aries 60° and 360° at latitude 40° N, photographs of the section visible to the bird, i.e., down to 50° distance from zenith. Sphere is seen "from above" so that compass directions appear "normal," i.e., east is at right of north, and west is at left. The arrows point toward planetarium north.

side. (See fig. 8.) These experiments show that the misinterpretations of the stellar patterns in the former series did not depend in any way on the amount of the angular shift of the sphere. With the same shift but other constellations, the reactions were quite different. No obvious mistakes occurred here. It

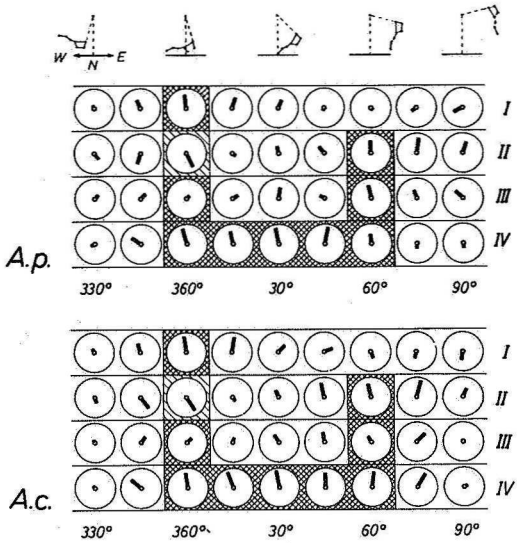

FIGURE 7. Mallard Q (top) and teal A (bottom), series I to IV, under simulated natural skies adusted to 9 hour angles of Aries with 15° (= 1 hr) intervals (40° N). Current training conditions are marked by cross-hatchings. During training, sphere was motionless in series I to III but rotating in series IV. Training direction = north = uppermost. Each vector represents 40 test cycles.

may be by chance that the birds reacted under both training patterns in about the same way. (It might be suspected that the birds were oriented by other than "stellar" cues in these particular series of experiments. The results at 330°, however, do indeed show dependence on the composition of the stellar sphere. Moreover, half of the tests were conducted under a reversed sky as described in ref. 7.)

A more thorough analysis of the experiments shown in figures 7 and 8 has to take into account the kind of motion of the sphere, i.e., the kind of change of its visible section, as well as the specific contents of the starry skies. Moreover, additional experiments with other variations of the stellar patterns will probably be necessary. Thus, no further

comments will be given here. It may be expected that understanding of these results will be facilitated at later stages of our investigations.

Partial Blocking of the Training Pattern

So far the section of the sphere visible to the bird was considered as a whole. We do not know, however, whether the animal reacts uniformly to all parts of the sky, or whether specific parts are more important than others, either depending on their location within the visual field or on their content of conspicuous stars or configurations of stars.

Our experimental setup allows two methods of blocking portions of the sky from view.

(1) The visual field of the bird can be reduced in size by partially covering the shielding cylinder with opaque disks or rings.

(2) Fields of projected stars can be extinguished by masking individual projectors.

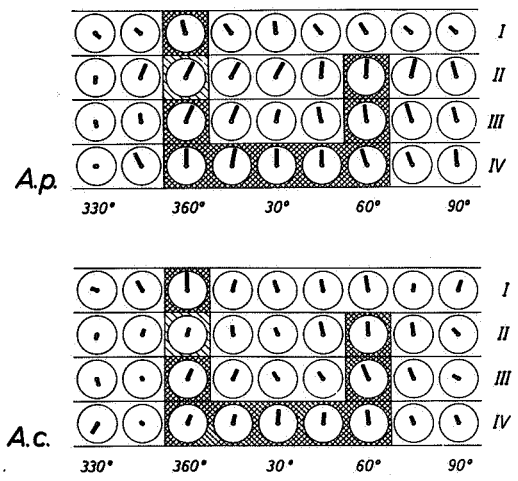

FIGURE 8. Mallard Q (top) and teal A (bottom), series I to IV, under artificial skies. Except for star distribution, procedure was same as in experiments shown in figure 7. (The naming of the hour angles is arbitrary.)

The following series of experiments were all made with teal A and all with the same training condition consisting of a motionless artificial (not simulating) starry sky not yet used for training or testing.

The results with the first kind of blocking are shown in figure 9. Clearly the responses are most concentrated when the test condition is identical with the training condition (A). On the other hand, with the shielding cylinder totally covered, the bird appeared totally disoriented (B). In the four situations with partial blocking, the scatter was in-

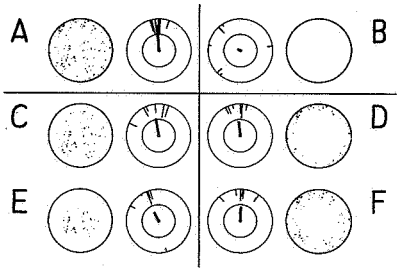

FIGURE 9. Teal A, artificial sky, blocking of the visual field by covering the shielding cylinder with rings and disks. Sphere fixed at a constant position. Star map is based on a photograph, but stars are enlarged in a rather schematic way. The sky is seen "from above" so that left and right is equivalent in both kinds of diagrams. In A, test condition equals training condition with an open view from 0° to 50° distance from zenith. In B, cylinder is completely covered. The open parts (distance from zenith) during the other tests are as follows: C, 0° to 40°; D, 40° to 50°; E, 0° to 30°; F, 30° to 50°. The other diagrams, representing the reactions, do not only show mean vector of total (with maximum length 1 being equivalent to radius of the greater circle), but also mean vectors of the individual tests, each of them consisting of a succession of 10 cycles. For these peripheral vectors, the scale is halved, maximum length being equivalent to distance between the two circles. (For sample size $n = 60$ [six tests] and significance level $P = 0.01$, the critical vector length is $a = 0.28$, i.e., somewhat more than half the radius of the smaller circle.)

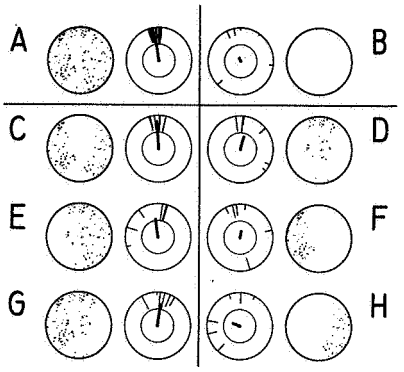

FIGURE 10. Teal A, the same artificial sky as in figure 9, part 1 of blocking experiments conducted by masking various combinations of the 11 individual projectors composing the visual starry sky as shown in A. Figures 10 to 12 refer to same test series. Tests were inserted irregularly into the training program. For further explanation see Figure 9.

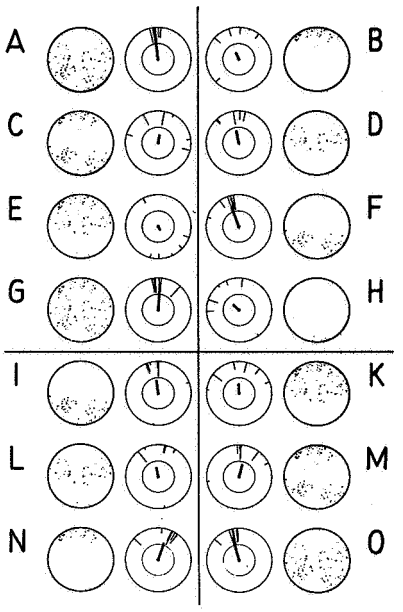

FIGURE 11. Part 2 of blocking experiments.

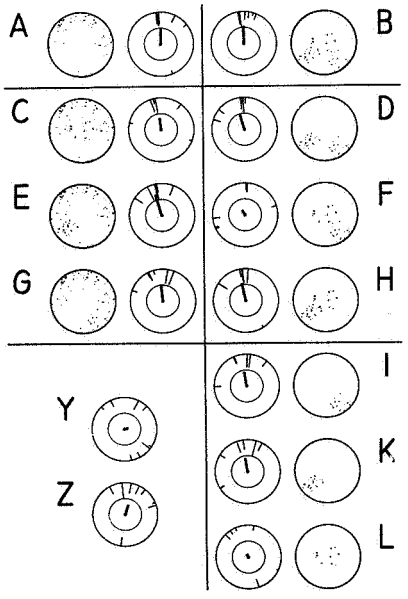

FIGURE 12. Part 3 of blocking experiments. For control in Y and Z no projector was covered, but the whole sphere was shifted around the polar axis by 60° "backward" (Y) or "forward" (Z), respectively, thus showing another section of the sky than during training. ("Latitude" was 30° "N.")

creased, but the maxima of heart rate were still accumulated in the direction of training (C to F). Thus, the bird was able to determine this direction by alternative use of either the periphery or the central part of the original field, though less accurately than with the whole field visible. In case E, a definite deterioration in performance is indicated.

With the second kind of blocking a larger series was conducted (figs. 10 to 12). The results can be used for merely tentative conclusions, for in many cases the reactions obtained during different tests were rather inconsistent, as indicated by the single vectors at the periphery of each diagram. It is unknown whether this inconsistency depends solely on changing states of the general motivation of the duck, or whether it depends in a more specific way on varying modes of recognition of the stellar patterns. With respect to some puzzling results, it should be born in

mind that controls against the bird's using other than stellar cues could not be applied during each individual test. [Control tests with reversed skies (ref. 7) were not conducted in this series in order to avoid creating smaller differences of visible fields by parallax.] Thus, although there is no evidence supporting such a suspicion, it cannot be entirely ruled out. In regard to the series as a whole, clear cases of disorientation demonstrate the dependence on the projected patterns (see, e.g., figs. 10B, 11E, 12L, 12Y).

In the figures the blocking conditions are arranged in pairs, the visible sky in the left column containing the blocked part of the sky in the right column and vice versa. In several cases the bird was obviously oriented under both conditions (see, e.g., figs. 10C and D, 11N and O, 12A and B, 12G and H), demonstrating that it was able to use both parts of the sky alternately, though there were differences either in accuracy (e.g., fig. 10C and D) or in direction (e.g., fig. 11N and O). In other cases, one part of the sky was obviously much more important for the bird's orientation than the other, as shown in figures 10G and H, 11A and B, 11E and F, 12 E and F.

It is not possible to discuss the whole variety of conditions and reactions in detail, but some lines of comparison may be selected. Figure 10 is used as a first example. In C, blocking of considerable parts of the sky—mainly overhead and in the training direction—did not affect the performance at all (compare A). With only the parts blocked in C visible, however, the bird was still oriented (D) though the scatter was increased and a small shift of direction indicated. Exposed to each of the two halves composing condition C, the duck appeared disoriented (F and H). Adding both these parts to D improved the performances as opposed to the results using part D alone (E and G).

Most puzzling are the reactions of the teal under the sky shown in figure 11E. There is not the slightest hint of a training response although huge parts of the sky were visible; more strikingly there were better responses although additional parts of the sky were blocked from view (see fig. 11D, K, L, N). Similarly figure 12I shows better results with a smaller part of the sky visible than figure 12F. If these are not chance results—and the fairly consistent responses in 11E do not support this idea—the only reasonable interpretation might be that under certain conditions the bird is more confused by looking at incomplete configurations than by entirely missing large parts of the starry sky.

Surprisingly good reactions are shown in figure 12I and K with very small parts of the stellar sphere visible. From these and many other cases it becomes clear that the distribution of illuminated parts of the sky or directional differences in brightness do not considerably affect the direction of the response.

DISCUSSION

Regarding the mechanism of pattern recognition, training may be a promising method of analysis because any arbitrary pattern of "stars" can be used. When considering the results, one has to bear in mind, however, that successful training can merely demonstrate what an animal is able to do, i.e., to perceive, to distinguish, etc. But it cannot tell us whether the animal makes use of the respective ability in its natural life. Thus, the experiments reported here cannot lead to a final decision on the mode of stellar orientation in nature. Yet they offer an opportunity for making hypotheses.

It has been shown that birds can learn to distinguish between different patterns composed of more than a thousand star-like spots. They have a remarkable capacity for

memorizing such patterns, and it is unimportant whether the distributions of the spots do simulate natural skies or not. Consequently it has been hypothesized at an earlier stage of these investigations (ref. 7) that migratory birds not only can learn but do learn and have to learn the specific contents of natural starry skies, together with their relation to the coordinates of the Earth. The decision had to come from experiments with birds raised isolated from view of the night sky and then tested with any kind of a "Kramer cage" method recording the spontaneous *Zugunruhe*. Excellent data of this kind were presented by S.T. Emlen at this symposium confirming the hypothesis by clear evidence.

In accordance with these results, my failure in recording oriented *Zugunruhe* in hand-raised European warblers (*Sylvia*) under a planetarium sphere (ref. 15) might be due to their negligible experience with the night sky. However, using birds of the same genus, Sauer (ref. 1) had recorded preferences of the normal fall migration directions —even with two individuals not experienced under the night sky, and with several hand-raised individuals kept indoors with limited possibilities to observe the sky. Thus, there are still incongruities in the results demanding further experimentation.

The question of whether bicoordinate navigation or compensation for displacements (for instance, by wind drift) by using nothing but stellar cues takes place in some species of birds (refs. 1,11, 16 and 17) is not much affected by the question of whether the "star-map" is learned or inherited, provided a bird is clever enough in "handling" the stars. Only in extreme cases with few or no stars of the experienced constellations available, would a bird necessarily fail to orient when depending on learned patterns.

During its first year of life, a migratory bird might be involved in a continuous learning process adapting it to the daily, seasonal, and latitudinal changes of the starry skies. Likewise, continuity in change of the appearance of the sky might be a precondition for successfully learning the whole variety of constellations. Once the bird has learned them, however, it does not need actual movement for recognition.

The essential clues by which particular views of the sky are recognized are still obscure. The blocking experiments show that different parts of the sphere can be used alternately. Thus recognition depends neither on the total aspect of the sky nor on a particular key star or constellation. On the other hand, the same experiments show that different parts of the sky are of different importance, as it was indicated in blocking experiments conducted by Emlen (ref. 10). One may hypothesize that the birds search for configurations that are more conspicuous than others and later on concentrate their attention on these selected patterns. This could be a way similar to our method of looking for well-known *Gestalt* stimuli.

At this point, investigation of actual pattern recognition should begin. For this, however, totally self-made "starry skies" allowing any variations would be desired. Since the projector we are using so far does not allow changes within a particular field of stars, further progress has to wait for a completion of our technical facilities.

SUMMARY

A conditioning method was used to investigate the orientational responses of ducks (mallard and European teal) as affected by manipulations of the stellar patterns in a planetarium. Under simulated natural skies, it was possible to train a bird to a particular direction successively under all positions of the rotating sphere at a constant latitude.

The responses were independent of the phase-relationships between local time, season, and appearance of the sky, provided that the bird had been trained under the particular section of the sphere some time before. The longest interval between training and testing was half a year, during which the bird learned to distinguish many additional patterns. No appreciable differences in learning and responding were found under artificial stellar patterns, never occurring anywhere in nature, as compared with simulated natural patterns. A mallard as well as a teal, each of them trained successively under two fixed skies of different appearance, misinterpreted these skies, obviously by trying to identify the two patterns with each other. Both birds were confused in the same way, which suggests that they evaluated these patterns quite similarly. Confusion ceased, however, when the sphere moved continuously from the one appearance to the other.

In another series of tests, parts of a fixed training pattern were blocked from view. It appeared that the bird was able to use different parts of the starry sky alternately to determine the training direction, though in most cases the reactions were less accurate than with the whole training sky visible. Some parts, however, seemed to be more important than others, causing disorientation when blocked from view. These experiments provide some clues to the mechanism of pattern recognition, but many more will be necessary for a real analysis.

DISCUSSION

QUESTION: Have you performed training experiments with rather simple arrangements of lights?

WALLRAFF: Yes, it is much easier to do than with stars.

ENRIGHT: Have you tried experiments with the Moon superimposed on the star pattern?

WALLRAFF: No.

WILLIAMS: In your series of tests, have you taken precautions to guard against day-to-day fluctuations? When you remove part of the sky, do you run that whole part and then go to the other part or do you run section C first and then D and then E?

WALLRAFF: The patterns were shown in irregular sequences, for example C_1, D_1, E_1 and then D_2, C_2, E_2 and then C_3, E_3, D_3 (C, D and E are the blocking conditions; the numbers mean 1st, 2nd, and 3rd test under the respective condition).

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Possible Steps in the Evolutionary Development of Bird Navigation

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DESPITE SCORES OF PAPERS and hundreds of experiments and tens of thousands of field observations there still exists much mystery about bird navigation. Some findings contradict other findings. Some investigators believe that studies of the homing pigeon will point the way to further understanding of navigation in migratory birds. Other investigators believe that only studies of wild, migratory birds will yield pertinent findings about this navigation.

Differences between the navigational attributes of species are recognized, but some investigators believe that there are basic clues used by all birds while others consider most migrant species to be somewhat different in their navigational attributes. Small wonder, then, that much confusion about bird navigation still exists among experts and laymen alike.

I believe that unnecessary confusion will exist until we organize the known facts about bird navigation on the basis of its probable evolutionary development. Moreover, if we can arrange experimental and empirical findings into their proper niches in the scheme of evolutionary development, we can greatly expedite planning for future research work on bird navigation.

I have endeavored in this paper to present my conception of the possible evolutionary course of navigational development in birds. Because of the broad scope of the topic, most of the information has been obtained from the literature.

REVIEW OF AVAILABLE CUES FOR NAVIGATION

As a prelude to a discussion of lines of possible evolutionary development in bird navigation, it is essential to review briefly ostensible and potential environmental cues available for bird navigation. The cues that fall into these broad categories are: landscape features, Sun as a compass, Sun for bicoordinate navigation, stars as a compass, stars for bicoordinate navigation, wind structure, and the Earth's magnetic field.

Landscape Features

Both experimental findings and field observations indicate that landmarks are the most fundamental cue in bird navigation. The use of landmarks by homing pigeons in the vicinity of their lofts has been noticed by most investigators studying this species. The

use of landmarks by wild birds in migration has been reviewed at length by Hochbaum (ref. 1); has been described for waterfowl by Bellrose and Sieh (ref. 2) and Bellrose (ref. 3), and for 38 species in the Sudan by Mathiasson (ref. 4).

In two different groups of experiments, bank swallows (ref. 5) and purple martins (ref. 6) were displaced varying distances from their nesting colonies. Observations were made on their directions of flight upon release and the times of return to their nest sites, under different sky conditions. Both investigators concluded that these diurnal migrants basically used landmarks as their cues for returning home.

Although the degree of use of the landscape is highly variable among many species, depending upon basic differences in mode of flight, range of flight, period of daily activity, and various other traits, all species appear to use landmarks for orientation purposes.

Sun Compass

I interpret a Sun compass as the ability of a bird to use the Sun for determining a fixed direction. A considerable body of evidence (summarized by Matthews, ref. 7, pp. 22–40) suggests that many migratory birds have a Sun compass. In addition to the many laboratory and field experiments that demonstrate the presence of a Sun compass in birds, certain displacement experiments provide circumstantial evidence of its presence.

Schuz (refs. 8 and 9) reported a series of experiments with white storks in which nestlings were transported from East Prussia west to the Rhineland. When East Prussian storks were released after the departure of Rhineland storks, they migrated over unfamiliar landscape, unaided by other storks, in a south-southeast direction, the standard direction taken by their parents.

Juvenile starlings displaced from Holland to Switzerland and from Holland to Spain (refs. 10 and 11) migrated in the standard direction but maintained their lateral displacement. Adult starlings behaved differently.

These displacement experiments demonstrate the ability of certain birds to maintain a direction of migration without the aid of known landscape features. Until there is contrary evidence, I believe it is only logical to assume that a Sun compass enabled these displaced birds to migrate in specific directions.

However, recent findings by Southern (refs. 12, 13) cast doubt on the presence of a Sun compass in all migratory birds. From experiments conducted with ring-billed gulls, Southern found no appreciable difference in directional response between birds tested under clear and under overcast skies. If a Sun compass is present in ring-billed gulls, it must be poorly developed.

Bicoordinate Navigation

The experimental evidence for bicoordinate navigation from the Sun is meager. It rests largely on a series of experimental releases made with Manx shearwaters under clear and under overcast skies by Matthews (refs. 14 and 15). Certain experimental releases of homing pigeons have also demonstrated bicoordinate navigation from the Sun (refs. 16 to 18); other releases of pigeons have shown only a directional type of orientation. Apparently the genetic composition of the pigeon stock, training, and loft site have influenced many of the varied results from pigeon experiments (ref. 18).

In addition to the direct experimental evidence for Sun navigation, I believe that certain displacement experiments provide circumstantial evidence that some birds have the capability of employing it. Perdeck's dis-

placement of adult starlings (ref. 10) from the Netherlands to Switzerland resulted in these birds flying back toward their original wintering area, and, in subsequent seasons, occupying their original range. In another displacement experiment, Perdeck (ref. 11) transported 900 adult starlings from the Netherlands to Barcelona, Spain. The results agreed with those of his earlier experiment: The adults again headed for their normal winter quarters.

Kenyon and Rice (ref. 19) displaced 18 Laysan albatrosses from Sand Island, Midway, to various areas of the north Pacific extending from Japan to the state of Washington. Fourteen birds returned to their nests over minimal distances of 2116 to 6629 km. Most of them averaged over 160 km per day, and one averaged 510 km per day.

Seven Leach's petrels were displaced from Kent Island, New Brunswick, to the coast of Sussex, England, a distance of 4795 km (ref. 20). Of the four that returned, the two fastest both had minimal speeds of 349 km per day; minimal speeds of the remaining two were 301 and 195 km per day. A Manx shearwater from Skakholm Island, England, released at Boston, Massachusetts, covered at least 4910 km at a speed of 393 km per day (ref. 21).

I believe that only through using the Sun to determine their longitude and latitude displacement from that of their distant homes could these pelagic species return so quickly. There is no other source of navigational cues known at present that would justify any other interpretation.

Star Compass

There is considerable information showing that many nocturnal migrants possess a star compass. A star compass may be defined as the determination of a standard direction from the location of stars alone. Astral navigation implies that a migrant is capable of determining longitude and latitude from star positions and correcting for any displacement, such as might be caused by strong lateral winds.

Sauer and Sauer (ref. 22) were the first to report that birds could utilize stars as an aid in navigation. Unaware of their work, Bellrose (ref. 23) reported on the one-direction orientation of mallards to the starry sky. In a series of papers, culminating in a study of the golden plover Sauer (ref. 24) sought to demonstrate that several species of birds were able to use astral cues for true bicoordinate navigation.

In a careful review of Sauer's early findings, Walraff (ref. 25) concluded that true navigation from stars had not been demonstrated. Since that time, many studies made on nocturnal orientation of birds have shown only a one-direction response to astral cues (refs. 26 to 29).

Moreover, Matthews (ref. 30) has reported that clock shifting of mallards affected a compensatory change in their diurnal orientation but not in their nocturnal orientation. Therefore, it is probable that directions of flight of nocturnal migrating mallards are obtained with reference to patterns of stars, rather than to the azimuth position of individual stars. This seems to negate the possibility of determining bicoordinate navigation from planetarium experiments.

Blue-winged teal are almost exclusively nocturnal migrants. Over several years we trapped blue-winged teal in central Illinois during September, and retained the juveniles for several weeks after the adult birds had departed the region. Band recoveries from the retarded released juvenile teal showed that they migrated toward the south and southeast, directions similar to those recorded for the species (ref. 31). Certain displace-

ment experiments also provide circumstantial evidence of a standard directional flight at night. During the fall of 1969 we air shipped 250 blue-winged teal to the Great Salt Lake marshes, Utah, 1850 km west of where they were trapped in central Illinois. Juveniles numbered 201 and were released at the Bear River National Wildlife Refuge; the 49 adults were released at the Ogden Bay State Refuge about 40 km to the south. The releases occurred on November 25 when no local blue-winged teal or cinnamon teal were in the region.

Omitting those band recoveries in the region of release, seven were reported at distant points within the following 6 weeks; all were over 640 km away in a south to south-southeast direction. Five of the seven recoveries were from juveniles and two were from adults. The blue-winged teal flew in directions appropriate to those used by teal in migrating from Illinois. There was obviously no evidence of compensation in direction of migration for their 1850-km westward displacement. I believe that these teal, represented by both adults and juveniles, used astral and possibly Sun cues to migrate in their customary direction.

The best indirect evidence for postulating true astral navigation that might occur in certain of the most sophisticated navigators is that given by Serventy (ref. 32, p. 170). He transferred 16 fledgling slender-billed shearwaters (which I calculated to be about 85 days of age from data presented by Serventy) in 1961 from nesting islands off the Tasmanian Coast to Fisher Island in Bass Strait. In the next few years, 3 of the 16 (19 percent) returned to Fisher Island, and 28 percent of the fledglings indigenous to Fisher Island returned there during the same period.

The period of sensitivity to locale imprinting apparently occurs in the slender-billed shearwater when it first emerges from its burrow at night to exercise its wings. This occurs about 14 days after the parent birds cease feeding the chicks when they are about 97 days old.

When Serventy (ref. 32, pp. 178–179) transferred 50 fledglings from other nesting islands to Fisher Island at the end of the desertion period (97 days after hatching), not one returned to Fisher Island, but 36 percent of the indigenous Fisher Island birds returned.

As I interpret Serventy's findings, there was only a 14-day difference in the ages of the young shearwaters between the two experiments. During this so-called 14-day period of desertion, prior to the young leaving the island, they are active only at night, and then only at the mouths of their nest burrows. Consequently, about the only cues available at that time would be those of the nocturnal sky.

The first returns of fledgling slender-billed shearwaters to Fisher Island (calculated in percent from data presented by Serventy, ref. 32, p. 175) for 209 birds are: 2 years, 1.4; 3 years, 23.0; 4 years, 47.4; 5 years, 16.7; 6 years, 9.6; and 7 years, 1.9.

During this long absence from the nesting island, the slender-billed shearwater migrates in a gigantic loop from west to east off the coasts of the North Pacific (ref. 33). It is truly one of the world's great migrants, and yet its navigation appears to depend primarily upon nocturnal cues obtained during a 14-day period.

Perhaps the exciting travel of one bobolink is another suggestion to true astral navigation (ref. 26). This bird escaped Hamilton on September 1, 1959, in San Francisco, California. It had been trapped at Kenmare, North Dakota, on August 9, 1959. On June 1, 1960, it was recaptured at the same banding station in Kenmare, North Dakota.

Wind Cues

The ability of birds to migrate at night when astral cues are obscured by dense cloud cover and landmarks are either invisible or indistinct has been shown by radar observations (refs. 3, 34, 35).

Radar surveillance of nocturnal migrants at night reveals little response to landscape features. In a study of bird migration at 20 U. S. Weather Bureau radar stations ranging over the entire eastern United States, the only evidence I saw of birds responding to landscape occurred between land and water along the Gulf Coast (ref. 3). Later, I observed another instance of birds responding to landscape. On the night of March 22, 1969, I watched flocks of Canada geese migrating northward on FAA radar, near Chicago, Illinois. Most of the geese were just to the west of Chicago. However, when they reached Lake Michigan, north of Chicago, many flocks turned abruptly east or northeast to head out over the lake (ref. 36, p. 281).

Birds migrating on nights when dense clouds obscure the starry sky are even less likely to view landscape than on clear nights. That poses the problem: What do they use for guidance when landscape and celestial cues are lacking?

The remaining environmental source of guidance information that is most omnipresent is the wind. Over a quarter of a century ago Griffin (ref. 37) suggested: "Birds might react to such phenomenon as prevailing winds and the characteristics of air masses. These are aspects of the environment bearing a certain relationship to geography."

Observing diurnal migrants, especially common chaffinches, in the Netherlands led Vleugel (refs. 38 and 39) to conclude that birds maintain a straight course by reference to the direction of the wind. However, at night without reference to other cues, birds could not sense direction if the wind were isotrophic. As pointed out by Nisbet (ref. 40), near the surface of the Earth the air is anisotrophic from friction with the Earth's surface features which produce wavelike currents of air correlated with the wind direction.

Most birds fly within 6100 m of the Earth's surface, which is well within the range of the turbulent wind pattern. With the addition of reference points on the Earth's surface, which are usually available, the nocturnal migrant is then provided with a minimum of two guidance cues.

Recent experiments with blue-winged teal (ref. 3, pp. 90–92 and unpublished observations) showed a similar degree of orientation under clear and under overcast skies. The direction taken by the experimental birds appeared dependent upon the temperature and wind direction.

In another series of experiments, Bellrose and Crompton (unpublished observations) placed groups of teal in two circular cages atop a 30-m tower. The teal in one wire cage were exposed to the wind; the view from the other cage was similar, but plexiglass prevented the birds from sensing the wind. After confinement in these cages for several days, the teal were released individually over unfamiliar landscape under overcast skies. Although birds from both groups tended to quarter downwind, those previously prevented from perceiving the wind flew markedly more tortuous courses and spread over a wider range than did the birds exposed to the wind.

Certain field evidence points indirectly to the use of wind as a potential cue in bird navigation. The tremendous loop migration of the slender-billed shearwater from Tasmania through the North Pacific is in accord with oceanic wind patterns (ref. 33). A similar loop migration by the greater shearwater

in the Atlantic Ocean from tiny Tristan da Cunha as far north as Greenland (ref. 41) also appears attributable to prevailing wind currents. Likewise, band recoveries from giant petrels indicate that they move westward completely around Antarctica with the prevailing winds of that region (ref. 42).

The known abilities of turkey vultures, Buteo hawks, and the white stork to take advantage of thermals in their extensive migrations is well documented.

Bellrose (ref. 43) compared the response of migrating birds to a variety of wind directions and speeds. This comparison was based on radar detection of the flight direction, speed, and altitude of migrants in relation to the wind direction and speed at similar altitudes. The birds observed on radar appeared to select wind characteristics that were favorable for their migration. The migrants' awareness of wind conditions led Bellrose (ref. 43) to postulate that winds were an additional source of directional guidance.

Although there is no experimental evidence to evaluate the role of wind in bird orientation, field evidence suggests that birds can use the wind as an aid in navigation. I anticipate that the degree of use would vary greatly among birds, depending on basic migration traits.

EARTH'S MAGNETIC FIELD

The report by Keeton (ref. 44)—that carefully controlled experiments of homing pigeons showed good homing under overcast skies—was most startling. It meant that to return with demonstrated facility and speed to their home loft these pigeons did not use the following cues: landscape features, the Sun, and the wind. Their release in an unfamiliar area negated the use of landscape features; the Sun was invisible throughout their flights; and they could not have diagnosed the relationship of the wind at the release site to the location of their home loft.

If Keeton's findings are eventually confirmed, it will mean that there is still another environmental cue available to birds for navigational purposes. Of the remaining sources of navigational information potentially available to birds, the most likely one is the Earth's magnetic field.

Over the past decade Merkel and Fromme (ref. 45) and Merkel and Wiltschke (ref. 46) have presented evidence that European robins in a covered enclosure were influenced in their choice of directions by weak magnetic fields. Investigators Perdeck (ref. 47) and Meyer and Lambe (ref. 48) could not elicit a directional response to magnetic fields in similar experiments.

However, Southern (ref. 12) reported that the directional selection of ring-billed gull chicks was adversely affected when the Earth's magnetic field was disturbed by solar flares. Therefore, evidence from several sources suggests that the Earth's magnetic field may be used by certain birds for directional information.

Eugene Mueller, electrical engineer and meteorologist with the Illinois State Water Survey reported[1] that the north-south gradient of the Earth's magnetic field extends undiminished in intensity through the atmosphere. However, anomalies are usually caused by local deposits of ferromagnetic materials and where ligneous extrusions high in magnetism penetrate sedimentary rocks weak in magnetism.

Variations in the geomagnetic field are weak and usually cannot be detected with a galvanometer above 3048 m (10 000 ft). In searching for anomalies on the Earth's surface, it has been found most expedient to use an airborne magnetometer about 760 m

[1] Personal communication from E. Mueller.

above the ground level. Therefore, if birds employ anomalies in the geomagnetic field as cues in navigation, generally the lower their flight the greater their ability to detect them. Over the oceans there are few anomalies in the geomagnetic field. Birds migrating over extensive oceanic areas would have recourse to only one reference in the geomagnetic field.

The many displacement experiments with Manx shearwaters, homing pigeons, starlings, and numerous species of waterfowl reveal their dependency upon celestial cues to depart the release areas. Because of the overwhelming evidence for the use of celestial cues, the use of geomagnetic force as a cue, if present, appears to be limited as to occasion and to number of species.

MIGRATION BEHAVIOR AS RELATED TO NAVIGATION

Among the several demonstrated and several potential cues available to birds for navigational purposes, the particular ones used by a given species are dependent upon the migration traits of the species. These traits are considered to be: (1) homing tenacity, (2) distance traveled, (3) diurnal-nocturnal periodicity of flight, (4) altitude of flight, (5) mode of flight, (6) feeding traits, and (7) social traits.

Homing Tenacity

The homing ability among most nesting sea birds studied is phenomenal. It is so well recognized that perhaps a few examples will suffice: The entire population of greater shearwaters, which roam to the far reaches of the Atlantic Ocean, nests on an island about 64 km in diameter in the Tristan da Cunha group (ref. 41). This small group of islands is isolated in the South Atlantic Ocean, some 1930 km west of Cape Hope, Africa, and a greater distance from South America.

The slender-billed shearwater returns from the northern reaches of the Pacific Ocean to nest on its specific island in Bass Strait between Australia and Tasmania. Indeed, Serventy (ref. 32, p. 180) reports that where there are several rookeries on an island ". . . no chick has settled on other than its own natal rookery." For 12 males, the average distance from natal burrow to first breeding burrow was 6.7 m; among 12 females the average distance was 7.6 m.

About 100 000 Laysan albatrosses nest on Midway Atoll and 130 000 on Laysan Island about 644 km to the east. Rice and Kenyon (ref. 49, pp. 532–533) reported that none of the thousands of albatrosses banded on Midway have been found on Laysan Island even though a diligent search was made there. Only a few of the black-footed albatrosses banded on Midway as chicks were found elsewhere; three were found nesting on Kure Atoll, 145 km to the northwest (pp. 533, 567).

Rice and Kenyon (ref. 49, p. 533) found that once they established a breeding territory, albatrosses returned to it season after season. Over half of all pairs nested within 1.3 meters of previous sites and none farther than 6.0 meters.

Austin (ref. 50) evaluated the homing of common terns to the several nest colonies on Cape Cod, Massachusetts. He concluded that young terns have a strong propensity to return to their natal colony; having once nested, most terns return year after year to sites previously used, site attachment increasing with age. Over half of the terns returning nested within 4.6 meters of their previous nest sites, the greatest distance was 19 meters.

Austin (ref. 51, p. 135) stated that most common terns migrate along the east coast of the United States as far as Cape Hatteras,

North Carolina, where they continue south over the Atlantic Ocean to the Bahamas. From there they pass through the West Indies to winter from Trinidad southward along the east coast of South America as far south as Rio de Janeiro.

No study of homing in oceanic birds has shown anything other than unbelievable preciseness of return. Therefore, until contrary evidence is presented, it must be assumed that other species of oceanic birds have comparable aptitudes.

Homing records among land birds are not as plentiful as among oceanic birds because of the great number of species, the general dispersed distribution among breeding individuals, their extensive breeding ranges, the small size of most species, and the difficulty of trapping breeding birds. Nevertheless, a slow but ever-increasing amount of information is being obtained on the homing ability of land birds.

One of the early findings of homing among passerines resulted from Hann's study (ref. 52) of the ovenbird. In a three-year period he found that 11 of 21 banded adult males (52.4 percent) and 13 of 23 banded adult females (56.5 percent) returned to nest on his study area near Ann Arbor, Michigan (op. cit., p. 153). Only 1 of 68 (1.5 percent) banded young returned to nest on the area. Studies in bird mortality have demonstrated that from 40 to 60 percent of the adults in most species succumb within one year. Mortality in nestlings is much higher. Therefore, a return approaching the reciprocal of the mortality rate would indicate an almost complete return.

A few ovenbirds winter in extreme southern United States, but most winter in Central America and south to northern Colombia, northern Venezuela, and the Lesser Antilles. Therefore, they make a moderately extensive migration.

Kendeigh and Baldwin (ref. 53, p. 116) believed that their banding data showed that 92.5 percent of all living adult birds returned to the general locality where they previously nested, but only 11.5 of the banded nestlings still alive returned. From an analysis of bandings of house wrens, Kendeigh (ref. 54, pp. 16–18) concluded that the large number of returns of adults in years following banding represented practically all living banded individuals. Of the 278 returning adult males, 84 percent nested within 300 meters of previous nest sites; 70 percent of the 276 returning females nested within the same distance. However, returning yearling house wrens ranged over a broader area, for only 15 percent of 154 banded yearlings occurred within 300 meters of their birthplaces.

Several species of swallows show excellent homing. Mayhew (ref. 55, p. 29) banded 4376 adult cliff swallows at breeding colonies near Sacramento, California. He recaptured 1668 (38.1 percent) the following year at the same sites, plus 368 (8.4 percent) at nearby sites. He banded 1098 nestlings of which 104 (9.5 percent) were recaptured the following year at their natal site and 77 (7.0 percent) at nearby sites.

Low (ref. 56) reported that 31 percent of the adult tree swallows that he banded returned to their previous nest sites, but only 11 percent of the young did so. Chapman (ref. 57) found that 38 percent of the adult tree swallows returned to his colony; only 4 percent of the young returned. The bank swallow appears to have the lowest return rate among the swallows: 12 percent of the adults and 5 percent of the young were recaptured by Bergstrom (ref. 58).

The black-capped vireo breeds among the arroyos of central Oklahoma, where Graber (ref. 59) studied its life history. It winters on the Pacific slope of the Sierra Madre Mountains of Mexico. Of the 17 adult males

banded, she recaptured 76.5 percent in subsequent years on the same study area. Female recaptures were somewhat lower: of 21 banded, 42.9 percent were recaptured. Mrs. Graber banded 30 young black-capped vireos, but none returned to her study area.

The Kirtland warbler has restricted breeding and winter ranges. Berger and Radabough (ref. 60, p. 184) reported on the banding of 161 adults and 296 young on its Michigan breeding grounds. The return rate in subsequent nesting seasons was: 52.9 percent of the adult males, 30.9 percent of the adult females, and only 2.7 percent of the young.

In a study made of piping plovers on Long Island, New York, Wilcox (ref. 61) banded 1173 adults and 969 young at their nest sites. I have recalculated his data (table 1 of ref. 61) to omit those years when the banding record was incomplete and to omit returns of 47 banded young that subsequently nested. Of the 893 adults initially trapped or carrying bands from previous years, 38.1 percent returned to nest the next year. This figure is minimal, because he estimated that 10 percent of the nests on the study area were not found and that he banded only 90.5 percent of the adults on the nests under observation.

Of the 47 young recaptured on nests, 34 returned to the area in which they hatched and 13 to areas 8 to 29 km away. Wilcox also trapped three young plovers banded elsewhere, which later nested on his area. One had moved 101 km east of its natal site, one 66 km east, and the third, 63 km east.

A large proportion of various species of waterfowl are known to return to their former nesting areas. Sowls (ref. 62, p. 37) found that the following adult ducks returned to the Delta Marsh area, Manitoba, to nest (by percent): mallard, 12; pintail, 39; gadwall, 37; shoveler, 42; and blue-winged teal, 14. Adjusting the return rate for mortality and for failure to trap some returning hens, Sowls concluded (ref. 62, p. 41) that most surviving adult hens returned to the marshes where they nested the previous year.

In central Illinois, Bellrose et al. (ref. 63, p. 665) captured 440 wood-duck hens on their nests, 1951–1962, of which 49.1 percent were found nesting in the same area the following year. Among 248 wood-duck hens banded as juveniles, only 6.5 percent were found nesting on their natal area the following year. Allowing for an annual mortality of 45 percent (adults) to 60 percent (juveniles) suggests that almost all surviving adult hens return to their previous nesting area as well as a moderate proportion of the surviving juvenile hens.

For many years Dexter (refs. 64 to 66) has been banding chimney swifts nesting in the same group of air shafts on campus buildings at Kent, Ohio. I interpret his reports as showing that all birds returning to these shafts had been banded by him as adults and/or nestlings in previous years.

From a banding study of mourning doves in central Missouri, Tomlinson *et al.* (ref. 67) concluded (p. 264) that ". . . most surviving adult doves return to the restricted area of the previous year's nesting." They found that only 13 of 411 doves banded as juveniles returned and concluded that homing occurs principally to first nest sites and rarely to natal sites.

In a study of homing of banded mourning doves to their nesting area near Madelia, Minnesota, Harris (ref. 68, p. 65) concluded: ". . . homing rates of approximately 100 percent for adult males and approximately 60 percent for adult females were obtained." He calculated that the return of nestlings was only about 2 percent.

Many species of adult land birds apparently exhibit an ability to home similar to

that of oceanic birds. There is certainly a pronounced difference in homing between the young of sea birds and those of terrestrial birds. However, the low rate of homing among young of terrestrial species should not be construed as a lack of ability, but it should probably be interpreted in light of their last visitation point prior to their fall departure. Bandings of many species of birds show that fledglings wander at distances much greater than do their parents prior to fall migration. Experimental displacement studies suggest that young birds return to the points they visited in response to the maturation of imprinted celestial and landscape cues.

A number of years ago we shipped young wood ducks hand-reared near Havana, Illinois, until 6 to 8 weeks of age to areas 280 to 320 km away (ref. 31). They did not return to their rearing area, but to their displaced area. I concluded (*op. cit.*, p. 35) that: "Young wood-duck hens exhibited a strong homing response to the area they inhabited during late summer and early fall preceding migration."

We also displaced adult and juvenile mallards from central Illinois to Great Salt Lake Basin in Utah, midway in their fall migration (ref. 31). The following fall, most band recoveries of adults were in their native flyway whereas, most of those mallards released as juveniles were recovered farther west (*op. cit.*, p. 30).

In Germany, Löhrl (ref. 69) displaced young collared flycatchers raised by hand, releasing them 90 km to the south in an area not inhabited by the species. The following spring, 19 percent of the males returned to their area of displacement. A smaller proportion of females returned, but some were missed. In 1956 Löhrl made another displacement release of 44 collared flycatchers that were just past their postjuvenal molt. The following spring, four, perhaps five, males returned (18 percent, assuming an even sex ratio). These birds had only about 2 weeks to become acquainted with their surroundings prior to fall migration. A third group of 68 flycatchers released later during the migration season did not reappear in the area of their displacement or their area of rearing.

It is apparent from Löhrl's experiments that there was a period of only 2 weeks when the young collared flycatchers were imprinted with the cues enabling them to return in the subsequent spring. This two-week period occurred just prior to their fall departure.

On the wintering ground of the northern waterthrush in Venezuela, Schwartz (ref. 70) displaced adults and juveniles from 6–65 km. Of the 4 adult and 14 juveniles moved, only the adults returned and some of the juveniles were subsequently found in their areas of displacement. Schwartz concluded that orientation ability is learned at the time first-year birds start their spring migration. I would amend his conclusion to: First-year birds are imprinted with their wintering-area cues prior to spring migration.

What are the cues available to collared flycatchers, northern waterthrushes, and other passerines prior to their first fall and spring flights? There can be little doubt that landmarks provide the detailed cues within their temporary home ranges prior to migration. Beyond that, celestial cues apparently provide the basic means enabling birds to reach the vicinity of their home ranges.

Certainly, Emlen's experiment (ref. 71) with 10 hand-raised indigo buntings point to the imprinting of astral cues. Of the four young buntings that never saw the sky until the experiment, one showed a significant southerly orientation, one slight southerly, and the other two were random. The three buntings that saw the outdoor sky for a month during the postjuvenal molt, showed a

notable improvement in selection of southerly directions. The response of Emlen's third group of buntings in his controlled laboratory experiment was remarkably similar to Löhrl's third experimental field release of collared flycatchers. Emlen held 3 buntings indoors until completion of the postjuvenal molt, when they were exposed to the sky throughout the migration season. Tests of orientation under the starry sky showed that only one bird consistently selected a southward direction; the other two birds showed no directional preference. It seems highly significant that collared flycatchers released by Löhrl after similar treatment failed to return. I believe that both groups had matured past the time of the effective imprinting of fall cues.

There is evidence that part of the low rate of return to natal areas by passerines and other terrestrial birds results from an imprinting of cues in a restricted period of maturation, prior to departure. The imprinting appears to be basically of a celestial nature, augmented by landscape. Therefore, the farther a bird migrates over featureless or obscured landscape, the more importance I attach to celestial cues in assessing navigational priorities.

Oceanic birds appear to have homing abilities superior to those of terrestrial birds. Based upon evidence at hand, I assume that the homing ability among different species of oceanic birds is similar, but that homing among different terrestrial species is on a comparable level.

Distance Traveled

The greater the distance that a bird travels in migration, the greater the feat of navigation. Further, on the basis of what we know today, navigation over the open sea out of sight of land is a greater feat than navigation over land.

Therefore, in ranking the evolutionary scale of development I have considered the distance flown over land and the distance flown over water. The distances flown in migration among species of birds were considered from the extreme northern boundaries of their wintering ranges. Banding data have indicated that individuals of a particular species that occur the farthest north in their breeding range are the individuals that winter the farthest south in their winter range.

Diurnal-Nocturnal Periodicity

Birds are basically diurnally oriented in their activity. Only a few species and proportionately fewer individuals are adapted for nocturnal feeding. Therefore, I consider that the more diurnal the migration activity, the more primitive are a species' navigational attributes. Conversely, the greater the nocturnal activity in migration (aside from the few nocturnal species) the greater are the navigational attributes of a species. Thus, I consider those species migrating predominately by day to be, as a group of species, more primitive in their navigational traits than those migrating, as a group of species, by both day and night. Similarly, I consider those species migrating almost exclusively at night, as a group of species, to be more advanced in navigational traits than those migrating about equally by day and by night.

There is, of course, a degree of overlap in the circadian activity of migration by all species. Some noted diurnal migrants, such as the purple martin, have been killed presumably at night at a TV tower (ref. 72, p. 60). All land birds crossing the Gulf of Mexico must often of necessity continue in diurnal flight until they reach land. George A. Hall has informed me[2] that several species of war-

[2] Personal communication from G. A. Hall.

blers migrate during the early morning hours along the ridges of the Allegheny Mountains in West Virginia.

On the basis of the activity of migrants that I have observed for over 30 years, on the basis of a diligent search of the reported bird kills at TV towers and ceilometers, after searching other literature for observations on migration activity, and after numerous discussions with colleagues, especially Richard R. Graber, I have attempted to classify many species of migrants as to their periods of migration activity. The greatest difficulty in classifying the day-night period of migration has been with oceanic birds. My impression from reviewing available literature is that most long-distance migrants among oceanic birds are equally active by day and by night.

Altitude of Flight

The higher a bird flies in migration, the less contact it has with the Earth. The less contact a migrant has with the Earth, the less opportunity it generally has to use landscape features (and/or the anomalies in the Earth's magnetic field if this proves to be a source of directional information) as part of its navigational system.

As every aircraft pilot knows, the greater the groundspeed, the higher the altitude required to make best use of landmarks. Visibility is also important in determining the most advantageous altitude for recognizing landmarks. At night and in rain or mist, landmarks may be visible only at very low altitudes. The nature of the landmarks also determines the relationship between their visibility and the altitude of flight.

Diurnal migrants appear to fly lower than nocturnal ones. Starlings, crows, various species of blackbirds, along with swallows, redheaded woodpeckers, blue jays, cormorants, white pelicans, cranes, hawks, and certain waterfowl make up the bulk of the diurnal migrants in midwestern United States, the region with which I am most familiar. Most of the starlings, blackbirds, redheaded woodpeckers, blue jays, and many of the swallows migrate at heights of 15 to 45 m above the ground, well below the "umbrella" of most radar surveillance. Starlings and blackbirds make up a large proportion of the total terrestrial birdlife in the United States.

Crows, gulls, and cormorants migrate at higher altitudes, usually from 30 to 300 meters above ground level. White pelicans and hawks have been observed migrating at altitudes of 300 to 900 m. Snow geese, cranes, and whistling swans have been reported frequently by pilots up to 2400 m, rarely as high as 3600 m, and more commonly at altitudes of 600 to 1500 m.

The enumeration of small birds at night in the landing lights of a small aircraft showed that most were at altitudes between 100 and 1500 m above the ground. A comparison of small bird and waterfowl targets on the same radar scope at Havana, Illinois, indicated that ducks migrated at higher altitudes during the night than did small birds. Among waterfowl, nocturnally migrating snow geese appeared at the highest altitudes. As identified by their speed of flight and their midsummer migration, shorebirds appeared on radar at Havana at consistently higher altitudes during nocturnal hours than any other group of birds.

Unfortunately, because we do not know the species relationship to altitude of most nocturnal migrants, especially the passerines, it is possible to assign to a species only the most general rank in navigational attributes based upon altitude of flight.

Mode of Flight

The navigational attributes of certain

species of birds are regulated in part by their modes of flight. Soaring birds, such as Buteo hawks, vultures, and white storks utilize thermals extensively in their migratory flights. Because thermals occur only during the daytime, these species are restricted to diurnal migration. If they maintain their soaring mode of flight, there can be no evolution into mechanisms enabling nocturnal navigation. As a group, soaring birds do not migrate as far as do birds with other flight characteristics.

Weak-winged flyers, notably rails and ground-seeking sparrows, probably of adaptive necessity to survival, evolved into nocturnal migrants. Usually, birds migrating short distances are diurnal migrants, or, at most, diurnal-nocturnal migrants. However, even though most weak-winged flyers migrate short distances, they are, as far as known, exclusively nocturnal in their migration. Therefore, they have reached a degree of sophistication in their migrational attributes far beyond that required by the challenge of their range. They probably were day migrants for a relatively short period in the span of geological time.

Feeding Habits

Birds feeding on the wing are regulated both in altitude and in daily period of migration activity by their sources of food. All species of swallows, and most species of oceanic birds, feed as they migrate. Thus, their routes of migration are in many instances at least partially determined by the sources of their food supply.

Long-distance oceanic migrants, such as the Arctic tern, greater shearwater, and Wilson's petrel appear to migrate where the upwelling of oceanic currents creates an abundance of food. It is well known that many creatures of the ocean move toward the surface at night. Consequently, most petrels and shearwaters, as well as some other oceanic birds, have adapted their feeding activity to nocturnal hours in order to exploit the greater availability of food (see Murphy, ref. 73, for detailed accounts).

Although swallows, particularly the barn and cliff, are some of the top long-distance migrants in the world, there is no adaptive advantage to their evolving into nocturnal migrants. Therefore, they remain, as they started, diurnal migrants.

I can find no information pointing to an oceanic bird as being an almost exclusively nocturnal migrant. Most petrels and shearwaters return to their nest burrows after dark, but over the ocean they are active by both day and night. Therefore, I assume that these birds navigate by both solar and astral cues on their extensive migrations. Winds must surely play an important role in their navigational scheme when overcast skies prevent the use of celestial cues.

Writing of the trans-Atlantic flight of the Arctic tern that he witnessed, Wynne-Edwards (ref. 41, pp. 328, 329) stated that

> there is not a vestige of a landmark of any description for two thousand miles, where the wind sometimes changes direction in a few hours and the sky is often completely overcast for days at a time . . . their sense of direction must be absolute, like that of a compass. . . .

He also reported (*op. cit.*, p. 326),

> In clear weather they fly between one and five hundred feet from the surface, but when beating to windward they often keep close to the wave crests.

On overcast days, how would these terns know windward from leeward? I believe that by keeping a reference between the angle of the wind and the waves, oceanic birds are able to maintain a particular course. Depending upon the magnitude of the waves and a

shifting wind, there is a considerable time lag. Hence, waves will continue in a set direction for some time before the wind gradually forces a change in the direction of their roll.

Landscape must surely play a limited role among the far-ranging pelagic birds that seldom see land except during their breeding season. Therefore, I place wind next to celestial cues in importance for navigation by these birds. Put simply, the more a bird is at sea, the less important is the role of landscape in its navigational system.

Social Traits

Birds that migrate singly rather than in flocks have evolved farther up the scale in sophistication of navigational traits. The single migrant does not have the reinforcement provided by the combined abilities of members of a flock (ref. 74), and, therefore, needs more refined abilities.

Some flocks, as in certain shorebirds, may be made up entirely of juveniles that migrate without the aid of adults. However, most birds migrate in flocks, composed of both juveniles and adults, in which case the juveniles appear to have recourse to the experience of older birds (ref. 75).

The advantage of adult leadership in navigation is especially evident in waterfowl. Because of adult guides, waterfowl not only return to the same breeding and wintering areas but also to the same migration areas (ref. 75). Among the several species of geese in North America, flocks are composed of family units that follow the same routes in migration as in previous years. Ducks do not travel as family units, but juveniles usually accompany adults from staging areas on the breeding grounds. The adults return to the same marshes that they visited the year previously, and so juveniles are indoctrinated in the sequence of water areas used by the adults they accompany.

In a system of point-to-point navigation, as shown by some species of waterfowl, landscape becomes more important than among migrants that are more flexible in locating their migration stops.

The fact that long-distance migrating Buteos (broad-wings and Swainson's) travel in large flocks while short-distance migrating Buteos (red-tailed, red-shouldered) travel singly or in dispersed malformed groups appears significant. By traveling in flocks, veteran birds are able to lead the way for young-of-the-year. As with other birds landscape is more likely to be important among species of hawks in which juveniles accompany adults.

The white stork is a soaring bird that travels in huge flocks for long distances, many from Central Europe to Central Africa. Schuz (ref. 9, p. 479) pointed out that in certain areas, storks radically change their direction of migration. I believe that landscape is the basis for the changes in direction noted one or more times in the course of their migrations.

Schuz's displacement (ref. 8) of young white storks in Germany points up the influence of old birds on the migration patterns of juveniles. I attribute the directional change in the migration of displaced East German storks to the influence of the adult storks in West Germany. When adults were available for guidance, the young East German storks became a part of the flocks of West German storks migrating southwestward. Young storks released later in the season, after the departure of the native storks, adhered to their innate southeasterly direction of migration.

Other traits being equal in the hierarchy of navigational sophistication, I place individual migrants, such as the flycatchers and yellow-billed and black-billed cuckoos, ahead

of flock-supported individuals. I rate flocks containing adults and juveniles ahead of flocks containing only juveniles. Flocks of several species of shorebirds are at times composed either of young or of adult birds. Most birds migrating in flocks contain both old and young birds.

HYPOTHESIS OF DEVELOPMENT

The foundation for exploring the various lines of navigational development in bird migration has been established in previous discussion: The navigational cues now known to be available to migrating birds have been appraised; the behavioral traits that affect the use of the several navigational cues have been evaluated.

Logically, bird navigational behavior has evolved from the primitive to the sophisticated. Most ornithologists agree with the concept that birds were nonmigratory before they evolved migratory habits. Today, in almost every order of birds, there are examples of nonmigratory birds, birds that migrate short distances, and those which make extensive journeys. There is not necessarily a relationship between phylogenetic evolution and the evolution of migration behavior. The loons and grebes are near the bottom of phylogenetic classification in birds, yet I believe they display sophisticated navigational behavior far in advance of that displayed by many of their more morphologically advanced members.

In order to establish an evolutionary hierarchy in navigation, it is imperative to understand the structure of navigation among nonmigratory birds. Unfortunately, few experiments of any kind have been made exploring the orientation mechanisms of permanent-resident birds. Permanent-resident birds displaced short distances show a low rate of return to their homes (summarized by Matthews, ref. 76, p. 22). Thus, house and European tree sparrows have given only 10 percent returns, and, at that, no farther than 9 miles (ref. 77).

Apropos to the navigational abilities of permanent residents versus migratory birds is a series of displacement experiments by Sumner and Cobb (ref. 78, pp. 317–319). They simultaneously released migratory and resident birds in several displacements of from 5.95 to 54.7 km from Claremont, California. A much higher return occurred among the migratory than among the resident species; all of the resident species either failed to return or only a small proportion did so.

Permanent-resident birds appear to move about their home ranges under adverse weather conditions. Even during snow showers, woodpeckers, titmice, nuthatches, and similar species search for food, indicating familiarity with their surroundings despite poor visibility. There can be little doubt that under such conditions birds employ knowledge of the landscape to fly from point to point. The failure of permanent residents to return home when displaced even short distances outside their home ranges points to their reliance on landmarks for local orientation.

I do not know of any studies evaluating the Sun compass among resident birds. The homing pigeon derives its ancestry from the sedentary rock pigeon, but man has artificially selected this species for homing capability to the extent that it differs genetically from its sedentary ancestors. Therefore, experiments demonstrating the Sun compass in the homing pigeon do not necessarily infer its presence in the sedentary form. The Sun compass appears so strongly genetically fixed among migrant birds I anticipate that some form will be found among nonmigratory species. The diverse directional flights taken by irruptive species (such as crossbills, Bohe-

mian waxwing, and snowy owl) over unfamiliar landscape indicate the probability of at least a rudimentary form of Sun compass among most nonmigrants.

Because soaring birds are so unique in their mode of flight and because oceanic birds are unique in the habitat they occupy, I place them in separate categories (fig. 1) from other birds.

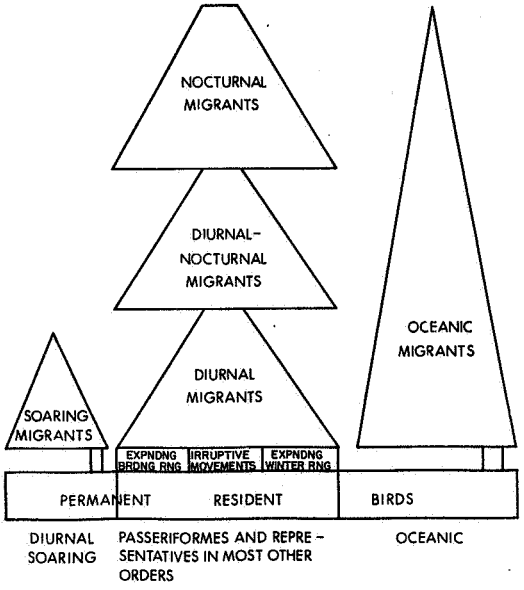

FIGURE 1. Model projecting possible evolutionary development of navigational mechanisms among soaring birds, oceanic birds, and passerines and allied species.

Migration in passerines and in the vast majority of other birds is postulated to have arisen from permanent-resident populations of birds that were in the process of expanding their breeding or their winter ranges, or were irruptive in their seasonal movements.

Partial migration probably represents the first step in the development of migratory behavior. Birds considered to be partial migrants are those in which a large proportion of the individuals are permanent residents and other individuals are migrants.

Even individuals among partial migrants may change their migratory state. Laskey (ref. 79) reported that a blue jay banded as a nestling migrated the first winter, remained the second winter, and migrated the third winter. Nunneley (ref. 80) concluded from a study of banded blue jays that some were permanent residents, some were transients, and others either summer or winter residents. She also noticed that some jays altered their migratory status between years.

Nice (ref. 81, p. 33) found that most of her marked song sparrows in central Ohio were either migratory or sedentary; a few individuals altered their migratory status in different years.

A list of the species of birds in eastern United States that best typify partial migration is given in table 1. The bulk of the partially migratory species are active in migration during the daytime. There are probably 10 times as many nocturnal species as diurnal migrants, so the proportion of partial migrants that are diurnally oriented becomes of even greater significance. The preponderance of partial migrants that move diurnally points to the first step in the development of navigational sophistication resulting from permanent residents extending their diurnal activities.

Diurnal-Nocturnal

As diurnal migrants extended their migratory ranges, certain species adapted their migration activity to both day and night to provide more time for feeding and/or to avoid losses from accipitrine predators. In regard to food supply, it appears significant that the only diurnal species with long migrations either feed on the wing (swallows) or are large birds (cranes).

An extension of diurnal migratory activity into partial nocturnal activity resulted in a further development of navigational sophistication. In order for birds to utilize nocturnal hours for migration it was essential for diurnally active species to adapt their navigational system to include nocturnal cues. And yet, by also migrating extensively during the day, diurnal-nocturnal migrants had cues (such as landscape, and the Sun) to correct for nighttime deviations from their selected courses.

Nocturnal

I believe that nocturnal migration behavior evolved from previous diurnal-nocturnal migration behavior. There is no well-defined line between diurnal-nocturnal and nocturnal migrants. Probably all nocturnal migrants continue in flight at some time during the early hours of daylight. Thus, the classification of migrants as nocturnal becomes one of degree. Perhaps a requirement for classification as a nocturnal migrant is that birds begin migration after sunset, whereas diurnal-nocturnal migrants begin migration either during the day or after sunset, depending upon the weather.

The adaptation of diurnal birds to nocturnal migration required a great evolution in navigational sophistication. Therefore, at present we are probably witnessing many stages in the development of navigational systems used by nocturnal migrants. Nocturnal migrants use cues available to diurnal migrants, in addition to the extensive use of more complex cues. It is important to recognize that, except for birds feeding on the wing, the passerine birds that migrate the farthest are all nocturnal migrants. Most intercontinental migrants in the western hemisphere are nocturnal in their migration within the United States.

TABLE 1.—*Species of Birds Considered to be Partial Migrants, Excluding Soaring and Oceanic Birds, in Eastern United States*

Diurnal migrants	Diurnal-nocturnal migrants	Nocturnal migrants
Common eider	Great blue heron	Wood duck
Willow ptarmigan	Killdeer	Red-breasted nuthatch
Redheaded woodpecker	Mourning dove	Bewick's wren
Horned lark	Flicker	Rufous-sided towhee
Blue jay	Mockingbird	Field sparrow
Gray jay	Robin	Song sparrow
Common crow	Cedar waxwing	
Black-capped chickadee	Eastern meadowlark	
Eastern bluebird		
Loggerhead shrike		
Starling		
Red-winged blackbird		
Brewer's blackbird		
Common grackle		
Brown-headed cowbird		
American goldfinch		

Soaring Migrants

Because their unusual mode of flight greatly influences their migration behavior, soaring migrants have evolved a navigational system distinctive from those of other groups. They are influenced in their routes of travel by bubbles of thermals and updrafts. The importance of continuity in the rising columns of air used by soaring birds results in their avoidance of expanses of open water. When groups of Buteos encounter the Great

Lakes in fall migration, they turn to the west (ref. 82, p. 84).[3]

After observing thousands of migrating hawks, particularly broadwings, at Duluth, Minnesota, Hofslund [4] believes that if specific points in the landscape are not used by hawks in piloting, then certainly they use the broad features of the landscape. Broad features of landscape are construed as directional axes of ridges, the breaks between woods and prairie and between woods and lakes, large river valleys, and similar features.

Mueller and Berger (ref. 83, p. 39) concluded from a band-recovery analysis and from field observations of migrating hawks that: "The system of navigation hawks use is crude and results in longitudinal and latitudinal displacements of considerable magnitude." They point out that on many days during the spring about 40 percent of the migrating hawks they observed were southbound in reverse migration.

However, their study embraced species of hawks that migrate comparatively short distances and did not include such long distance migrants as turkey vultures and broad-winged and Swainson's hawks. Extensive flights of Swainson's hawks have been recorded across the southern Great Plains. At Hutchinson, Kansas, Cruickshank (ref. 84) counted 3400 in 1½ hours, moving due south, and remarked about the generally featureless landscape. In south Texas, Fox (ref. 85) saw 25 000 cross a 0.4-km (¼-mile) line, and estimated that perhaps several hundred thousand Swainson's hawks passed directly south in a well-defined channel about 6.4 km wide on October 6, 1953. He commented on the gently rolling prairie landscape and on the flight crossing the rivers at an angle.

Large flocks of broad-winged hawks have been noted migrating through Panama in early October (ref. 86). Near Veracruz, Mexico, Bussjaeger, et al. (ref. 87) found a large northward migration of turkey vultures on March 27, 1966. One flock was 5 km long and contained several thousand members. They were restricted to the coastal lowlands.

The Nile River appears to form an important route for migrating white storks. Accounts by Mathiasson (ref. 4) and Reed and Lovejoy (ref. 88) point to the importance of the Nile landscape. Migrating storks follow the Nile Valley closely until they reach the lengthy Dongola bend, where they cut overland to reach the river again (ref. 88, p. 49).

Mueller and Berger (ref. 89, p. 55) suggested that birds utilizing updrafts in flight are especially subject to wind drift. Hofslund's (ref. 82, p. 85) observations have shown that hawks in migration quarter into the wind, shifting their position with the slightest change in wind direction. However, he did not rule out thermal drifting, and postulated that drifting of thermal bubbles on westerly winds might displace hawks eastward from their standard southwestern direction of flight, thereby concentrating them along the north shore of Lake Superior.

Mueller and Berger (ref. 90, pp. 184–185) observed reverse migration of hawks in the fall on only two occasions. Both days were overcast. Apparently a warm front with its initial southerly winds resulted in most of the hawks moving northward, a reverse direction. They observed reverse flights among hawks more frequently in the spring, often when the skies were clear (ref. 83, pp. 35–37). They believed that these birds were reorienting, possibly to their nesting areas. From Mueller and Berger's fall observations (ref. 90) it seems probable that migrating hawks in spring are carried astray by wind when days are overcast and reorient toward

[3] Personal communication from P. B. Hofslund.
[4] Also personal communication from P. B. Hofslund.

their home areas when the Sun becomes visible.

Thus, it appears that soaring birds use the Sun, the landscape, and the wind in navigation. We postulate that as distance of migration increases, the use of the Sun and the wind for orientation increases and the use of the landscape decreases.

Oceanic Migrants

Oceanic birds appear to have the greatest homing ability among all birds. As an ecological entity, they appear to have a larger proportion of long-distance migrants than do terrestrial groups. The navigational ability of oceanic birds appears on a higher evolutionary scale than that of other birds because oceanic birds make little use of landscape features. I postulate that landscape is the most fundamental cue used in bird navigation with other sources of directional information being more advanced.

The problem among oceanic birds is to differentiate between diurnal, diurnal-nocturnal, and nocturnal development of navigational cues. It is apparent from the activity patterns at sea that there is an advanced state of nocturnal navigation present in certain petrels and shearwaters. Although they also may be active in the daytime, I believe that their star compass must be on a level equal to, if not greater than, that of the most advanced nocturnal migrants among terrestrial birds.

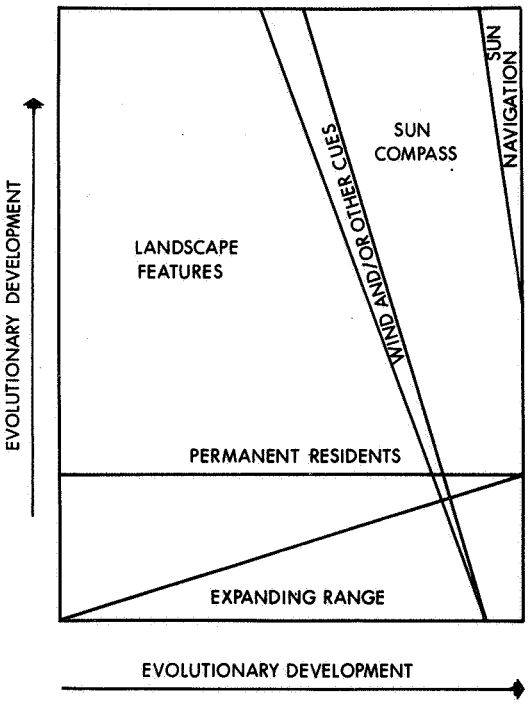

FIGURE 2. Postulated schematic diagram of gradual change in comparative use of navigational cues by diurnal migrants. As birds progressed from permanent-resident status to that of increasingly long-distance migrants, navigational sophistication became adaptive to their needs.

EVOLUTIONARY DEVELOPMENT OF CUES

Diurnal Migration

Figure 2 shows a model of my concept of evolutionary development among terrestrial birds with diurnal migration activity. From permanent residents, depending almost exclusively on landscape feature, the first partial migrants that evolved also utilized landscape features, perhaps with an assist from their Sun compass.

In figure 3 I have attempted to give examples of increasing sophistication in navigational ability among birds with diurnal migration traits. My criterion for greater sophistication of navigational ability among diurnal migrants is based largely upon the increasing distance flown in migration. The migrational behavior of several species are examined to illustrate the possible development in navigational sophistication.

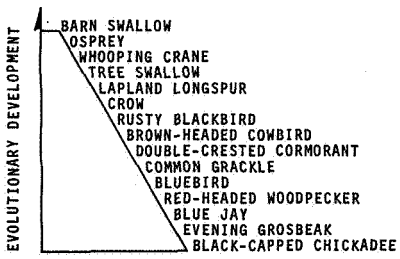

FIGURE 3. Diurnally migrating species of migrants are arranged to represent examples of increased sophistication in navigational attributes. Of those listed, the black-capped chickadee is considered the most primitive migrant and the barn swallow the most advanced migrant.

The black-capped chickadee is a permanent resident bird that probably only recently developed partial migratory behavior. An excellent review of chickadee migration is given by Bagg (ref. 91), which indicates an alternate-year intensity in the abundance of migrants. Over 30 000 black-capped chickadees have been reported in the fall, in each of 2 years, flying along the shore of Lake Ontario (op. cit., p. 12). Their response to water barriers is to fly along shorelines to where short water crossings or land bridges enable them to migrate in their preferred direction. When attempting a water crossing, they fly into the wind; observers interpret this heading into the wind as a downwind option to return if the crossing attempt fails. Thus the chickadee shows an awareness of the wind in relation to the landscape.

Figure 4 shows some band recoveries for the black-capped chickadee. The recoveries are both north and south from points of banding and at distances of 160 to 800 km. This is evidence that a bird once considered a permanent resident has developed a partial migration.

The blue jay, too, was once considered a permanent resident. However, in the last three decades numerous notes and articles have appeared about their migratory habits from Nashville, Tennessee (ref. 79), on the south, to Quebec on the north (ref. 92).

Blue jays migrate more extensively and farther than the black-capped chickadees. Band recoveries from the files of the Patuxent Banding Laboratory reveal that a number of blue jays have migrated 1600 km or more and many have migrated over 800 km.

We have traced one blue jay flight path through central Illinois for almost 160 km (fig. 5). Blue jays have been known to follow this flight path which in places is no more than 90 m wide for at least 6 years. It doglegs around the cities of Havana, Peoria, and Pekin. In this stretch of its migration, the movement is from tall-tree top to tall-tree top and from woodlot to woodlot. The migration period extends over 2 months both in fall and spring. Although several thousand jays follow this path in the spring, fewer use it in the fall. There appear to be many more routes used in the fall.

The important point as regards naviga-

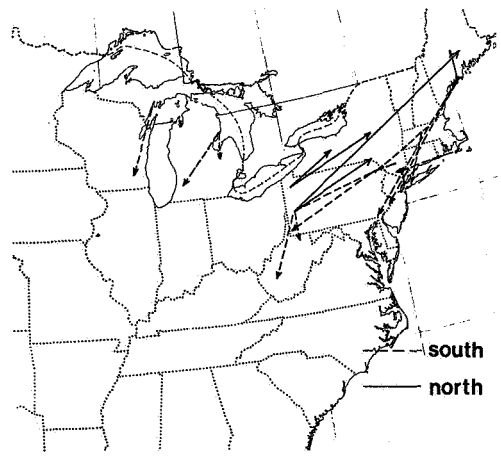

FIGURE 4. Band recoveries of black-capped chickadees in eastern United States as reported by Bagg (ref. 91).

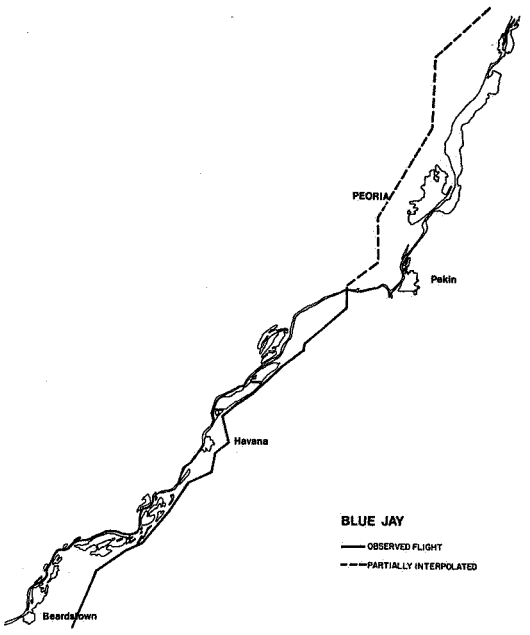

FIGURE 5. A heavily used spring migration route of the blue jay through central Illinois.

tion is that whether the day is overcast or clear makes little difference in the volume of migration. This fact was also noticed by Broun (ref. 93) at Hawk Mountain, Pennsylvania.

We have noticed, as has Schorger (ref. 94), that the velocity and direction of the wind greatly influence the magnitude of migration. Schorger noticed that migrating jays adjusted their heading in keeping with the direction of the wind in order to maintain the same track across Lake Mendota.

Our field observations on migrating blue jays appear to justify these conclusions: The blue jay is advanced in navigational development over the black-capped chickadee. The blue jay relies heavily on landmarks to follow the same narrow course year after year. The Sun compass is probably needed only to roughly determine north and south and is probably not well developed. The blue jay recognizes wind direction and velocity, and is aware of their value in crossing wide expanses of water.

I ranked redheaded woodpeckers higher in navigational development than blue jays because these woodpeckers usually migrate singly rather than in flocks. They, too, follow narrow flight paths at low heights. The same flight paths have been used year after year by adults. The young-of-the-year appear to observe the flight course taken by adults, and their Sun compass may be sufficiently developed for them to adhere to a standard direction.

All the blackbirds and the starling have similar migration behavior and often migrate together. The principal difference between these species in their rank of navigational development is their relative distance of migration. We have observed blackbirds migrating in a standard direction over 48 km under overcast skies at altitudes of 7.6 to 15 meters (25 to 50 ft), so low that landmarks would seem to have minimal value. I believe that under these circumstances a combination of landscape and wind direction was used to maintain the same flight direction.

As shown by Kramer's (ref. 95) orientation experiments with starlings, this species has a well-developed Sun compass. It is likewise apparent, from their extensive migration under overcast skies, that they do not always need it.

The common crow is placed higher in the hierarchy of navigational development than the blackbird because it migrates at higher altitudes and in smaller groups.

Whooping cranes migrate in family groups along a narrow well-defined corridor for 3620 km. They migrate at unusually high altitudes. For these reasons I have placed them near the pinnacle of diurnal navigational achievement.

Ospreys migrate singly, and some migrate

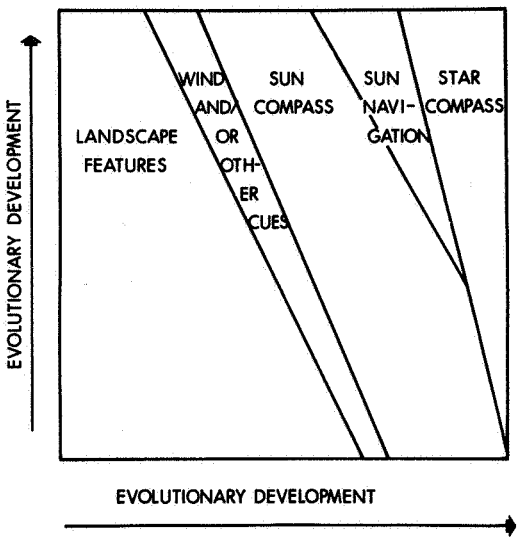

FIGURE 6. A postulated schematic diagram of gradual change in comparative use of navigational cues among diurnal-nocturnal migrants as evolutionary development progressed.

as far south as central South America. The fact that young ospreys apparently make extended migration flights without the guidance of adults suggests their probable ability to conduct true Sun navigation.

The barn swallow makes the longest diurnal flight of any terrestrial bird, from northern Alaska to southern Argentina. Many travel in flocks but some migrate singly. Experimental displacement of barn swallows in Europe (ref. 76, pp 26–27) showed reasonably good homing from long distances. Such homing over unfamiliar landscape suggests that they are able to use the Sun for bicoordinate navigation. On the basis of this cursory evidence, I have ranked the barn swallow at the peak of navigational sophistication among diurnal migrants.

Diurnal-Nocturnal Migration

As a group, diurnal-nocturnal migrants travel farther than diurnal migrants. Landscape features play an important role in the early stages of navigational evolution, but become less important in the advanced stages (fig. 6). The Sun compass is probably present in a good state of development in species that are above the migrational level of the mockingbird. The ability to use the Sun for navigational purposes probably has evolved about midway along the line of developing sophistication. Because of their ability to migrate by night, this behavioral group has a star compass that becomes of increasingly important as the distance of migration increases.

My concept that species of diurnal-nocturnal migrants represent a progressive development in sophistication of cues used in navigation is shown in figure 7. The mockingbird is only a slight partial migrant and until recently was considered a permanent resident. Banding, visual observations, and TV tower kills (ref. 72, p. 61) attest to a part of its population being migratory. Richard Graber and I have seen it migrating diurnally in Illinois, and the 26 killed at a TV tower near Tallahassee, Florida (op. cit.) point to nocturnal migrations.

As the flight distances increase, I postu-

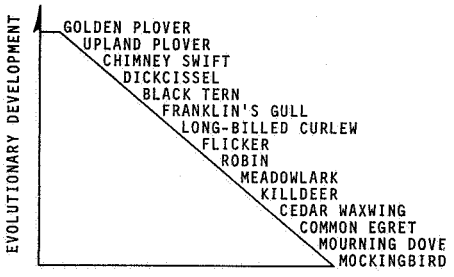

FIGURE 7. Diurnal-nocturnal migrants arranged to represent examples of increased sophistication in navigational attributes. Among those listed, the mockingbird is considered the most primitive migrant and the golden plover the most advanced migrant.

late increasing demands in navigational ability and increasing nocturnal activity. Because of a lack of knowledge, I have probably positioned some species improperly. For example, perhaps the Franklin's gull and the chimney swift are only diurnal migrants. I placed the Franklin's gull as a nocturnal-diurnal migrant on the basis of migrants observed still flying south at dark across the farm country of Nebraska. The chimney swift was classed as a partial nocturnal migrant on the basis of 19 killed at night at a TV tower in Florida.

Nocturnal Migration

Among species of birds that are almost exclusively nocturnal migrants, landscape features are of minimal value (fig. 8). Radar studies suggest that landscape plays a part in their navigational systems largely at the times of departure and arrival. During the night there are only a few records of birds altering their courses because of landscape.

A Sun compass is present but the ability to use the Sun for true bicoordinate navigation is postulated as providing the basis for any course alteration resulting from nighttime displacement. Because of their nocturnal activity, a star compass is well developed and becomes increasingly so as distance of migration increases. It is conceivable that in species with the most advanced forms of nocturnal navigation, we may find evidence of the use of stars for bicoordinate navigation.

Radar studies suggest that nocturnal migrants recognize wind patterns, which they utilize in their navigational system when other more obvious cues are unavailable. Without landscape, the characteristics of winds would be more difficult to sense at night than during the day. Accordingly, I have placed more emphasis on this source as a cue among nocturnal migrants than among diurnal migrants.

Figure 9 shows possible examples of nocturnal migrants at various stages in the development of a sophisticated navigational system. The red-breasted nuthatch appears to be the nocturnal counterpart of the diurnal

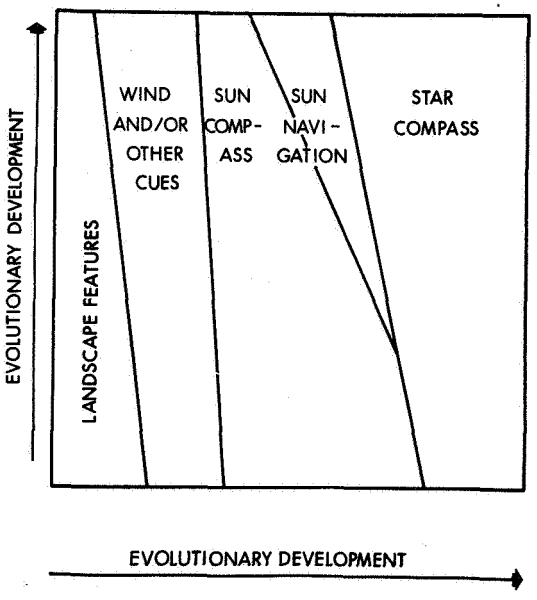

FIGURE 8. Postulated schematic diagram of gradual change in comparative use of navigational cues among nocturnal migrants as evolutionary development progressed.

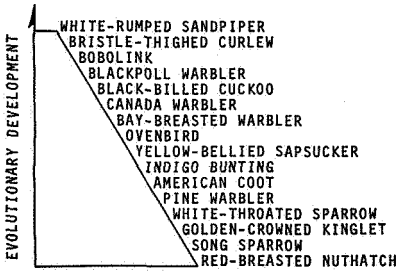

FIGURE 9. Nocturnal migrants arranged to represent examples of increased sophistication in navigational attributes. Of those listed, the red-breasted nuthatch is considered the most primitive migrant and the whiterumped sandpiper the most advanced migrant.

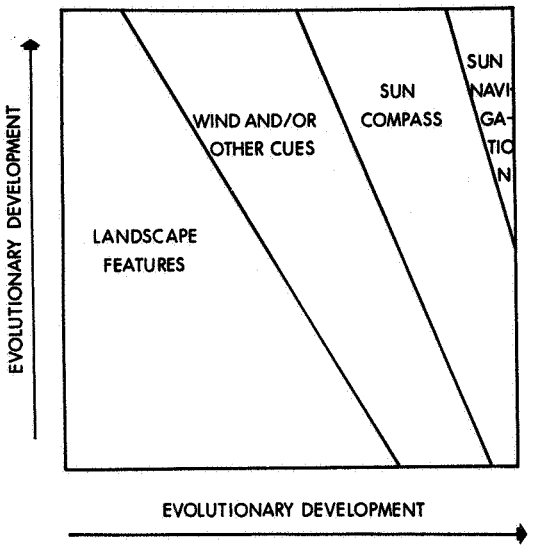

FIGURE 10. Postulated schematic diagram of gradual change in comparative use of navigational cues among migrants with soaring flight as evolutionary development progressed.

black-capped chickadee. It migrates somewhat irregularly but over longer distances than the chickadee.

Song sparrows are partially migratory in the southern part of their breeding range, but almost completely migratory in the northern part of their range, which extends to the Yukon and Alaska. From the level of the song sparrow through the level of the coot, increasingly smaller segments of their populations are partially migratory. There are increasingly greater distances between the breeding and wintering ranges from the indigo bunting to one of the champions of long-distance migrants, the white-rumped sandpiper.

The black-billed cuckoo deserves a high rank in the navigational hierarchy not only because of the long distance it migrates but also because it appears to migrate singly. Perhaps I have erred in classifying bobolinks, bristle-thighed curlews, and white-rumped sandpipers as nocturnal migrants. Bobolinks are known to migrate by day, but they apperar to be largely nocturnal migrants, judging from their nocturnal calls and the kills at TV towers. Little is known about the activity patterns of the two uncommon shorebirds (bristle-thighed curlew and white-rumped sandpiper), but based upon observations of other long-distance migrating shorebirds, I assume that they are nocturnal migrants except over a hostile environment, such as the ocean.

Soaring Migration

As previously discussed, migrants that depend upon soaring are more the captives of wind conditions and diurnal activity than are birds with other flight modes. Therefore, the wind, the landscape, and the Sun compass probably play important roles in their navigation (fig. 10).

Some species of soaring hawks are permanent residents in extreme southern United States and throughout Mexico. The black vulture and red-shouldered hawk are largely permanent residents, but part of their populations are migratory (fig. 11). The ferruginous hawk has both a sizable permanent and a migratory population.

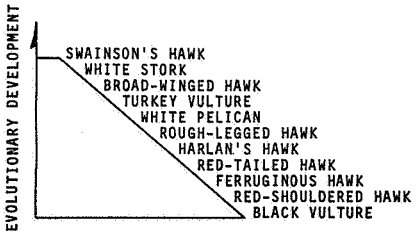

FIGURE 11. Migrants with soaring flight arranged to represent examples of increased sophistication in navigational attributes. Among those listed, the black vulture is considered the most primitive migrant and the Swainson's hawk the most advanced migrant.

Soaring birds that do not migrate far, such as the black vulture and the red-shouldered hawk, probably depend upon landscape more than any other environmental cue (fig. 11). As distance of migration increases, it is postulated that landscape became of lessening value and the Sun and wind of increasing value for navigational purposes.

The breeding grounds of the Harlan's hawk are well separated from its wintering grounds, and it appears to migrate along a rather restricted corridor. Swainson's hawks make an astonishing long-distance migration, some from as far as Alaska to southern South America.

I believe that certain long-distance migrants may be able to use the Sun for bicoordinate navigation, but this is only speculation until some experiments can be conducted to evaluate this point.

Oceanic Migration

Migration by oceanic birds may be classified as inshore, offshore, and pelagic. The closer a migrant adheres to the shore, the greater its potential use of landscape for orientation (figs. 12 and 13). The more pelagic the species and the greater the distance of migration, the less importance landscape features would assume in its navigational system.

Because of the tremendous distances flown by a number of pelagic species, almost entirely out of sight of land, their ability to use the Sun for bicoordinate navigation must be unequalled in the avian world. The great awareness of wind possessed by oceanic birds implies that it would serve as an increasingly important navigational aid as distance from shore and distance of flight increase.

Most petrels and shearwaters feed at night, indicating their ability to use the stars for at least directional guidance if not for bicoordinate navigation. I suspect that if any oceanic birds can perform astral bicoordinate navigation, they are the Wilson's petrel and the greater and slender-billed shearwaters.

Many oceanic birds are nonmigratory. In tropical regions the brown booby, blue-footed booby, and noddy terns are good examples.

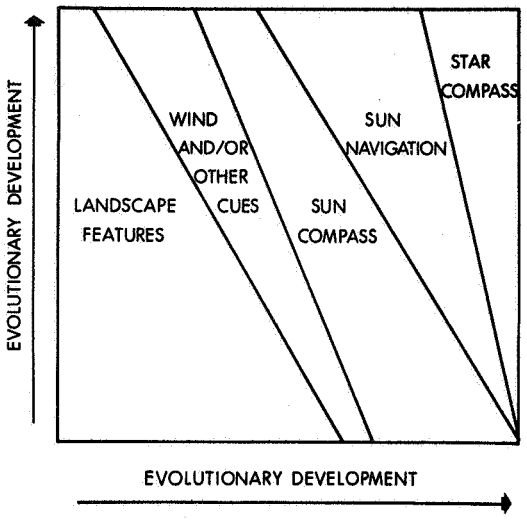

FIGURE 12. Postulated schematic diagram of the gradual change in comparative use of navigational cues among oceanic migrants as evolutionary development progressed.

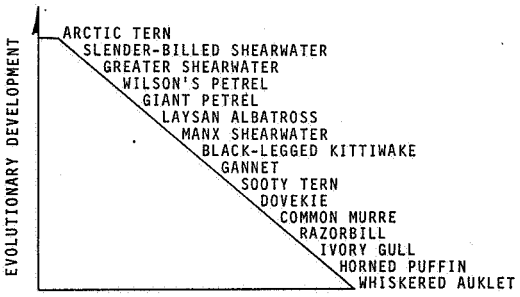

FIGURE 13. Oceanic migrants arranged to represent examples of increased sophistication in navigational attributes. Among those listed, the whiskered auklet is considered the most primitive migrant and the Arctic tern the most advanced migrant.

According to Orr (ref. 96, p. 141), not all shearwaters are migratory. Those breeding in tropical areas do not leave the general vicinity of their nesting islands. Unlike the Manx shearwater in the Atlantic, the Pacific coastal population spreads out only a few hundred km from breeding areas.

Many of the puffins and auklets nesting in Arctic regions migrate not at all or only short distances. From species such as these with very little demand on navigational mechanisms, oceanic birds migrate farther and farther until they have reached the opposite ends of the world. Examples of the increasing migration range among oceanic birds are given in figure 13.

As the distances of migration have increased among oceanic birds, I believe that there has been a comparable development in navigational sophistication, as shown in figure 12.

The Evolution of Navigation in the Anatidae

I have selected one family of birds, the Anatidae, to illustrate possible steps in the evolution of navigational development, independent of morphological development. Figure 14 shows the relationships of various species of waterfowl to navigational cues.

Nonmigratory waterfowl are exemplified by the mottled duck and the Florida duck. Because they move only short distances, they probably depend largely on landscape features, assisted by a Sun compass, for basic directions. The spectacled and king eiders are diurnal migrants with short migration routes. The tremendous passage of king and common eider along the Alaskan coast near Point Barrow has been reported by Thompson and Person (ref. 97).

Common and surf scoters migrate diurnally considerably greater distances than do the eiders. In all likelihood, these sea ducks require only landscape features and a Sun compass to meet their navigational needs.

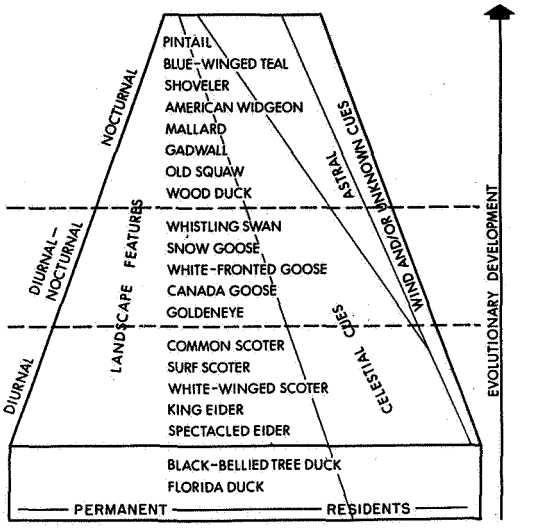

FIGURE 14. Steps in evolutionary development of navigational sophistication as postulated for one family of birds, the Anatidae.

The common goldeneye illustrates the next step in navigational development, because it migrates partly by night as well as by day. Migration at night requires that the goldeneye be able to use certain star patterns for directional information. The Canada goose migrates almost equally by day or night, and generally migrates farther than the goldeneye. White-fronted and snow geese migrate farther and higher than do most Canada geese, and appear to be more nocturnal in their migration activities. Therefore, they are classified as more advanced than the Canada goose in their navigational sophistication.

Some whistling swans migrate from the Yukon–Kuskokwim Delta in Alaska to Chesapeake Bay, Maryland. On this long migration in the fall, they make few stops, migrating by both day and night. At certain points in their migration, they make significant changes in direction of flight. Most, if not all

of these turns occur where there is a prominent landmark in the form of a body of water. Thus, landscape features are important as turning points in standard directions. Their migration during nocturnal hours implies the presence of an astral compass, and, when the stars are invisible because of clouds, an ability to use the wind.

Most non-sea ducks are more nocturnal in their migration habits than they are diurnal. However, at times species migrating in late fall, such as the mallard, are induced by severe weather to initiate migration during the day. They migrate under overcast skies, which suggests that the wind is a cue used to maintain a particular line of flight.

The wood duck makes especially short flights, the mallard somewhat longer, with the widgeon, shoveler, blue-winged teal, and pintails making increasingly longer migrations. Blue-winged teal frequently cross the Gulf of Mexico, and, perhaps, the Caribbean Sea to reach winter grounds in Venezuela and Colombia. Some pintails fly from Alaska to the Hawaiian Islands.

It may be significant that in conducting orientation experiments under overcast skies, we have found that the blue-winged teal, a long-distance migrant, and the mallard, a comparatively short-distance migrant, respond differently to the wind. The mallard flight is random regardless of wind direction, but the blue-winged teal quarters either upwind or downwind so that all individuals released separately in an experiment show similar flight directions. This is further evidence that the farther a bird migrates the more sophisticated its navigational system.

Orientation experiments that we made with Canada geese, mallards, blue-winged teal, and pintails (ref. 98) indicated that all four species are able to use the Sun and stars for directional purposes. None have shown bicoordinate navigation by day or by night.

DISCUSSION OF RESULTS

The behavior of migrating birds in the air space can tell us much about the cues that are used in navigation and how they may have evolved. The literature reveals that unfortunately there is a great dearth of information about the migration behavior of even common birds. In many cases it is difficult to find information relative to the most obvious behavior patterns, such as whether a bird is a diurnal or a nocturnal migrant or flies singly or in flocks. There is only scant information on such complex subjects as altitude of flight, course of migration, distance of flight, and response to sky and wind conditions.

With all of the laboratory-type experiments evaluating celestial cues used by migratory birds, it is frustrating to find not one experiment with a nonmigratory species. To understand properly the mechanics of bird navigation, the orientation capabilities of nonmigratory birds must be thoroughly analyzed. Once a base of orientational capability has been established for representative species of nonmigrants, then experimental and empirical findings on migratory species can be meaningfully classified and evaluated.

I do not believe it is necessary to be concerned about the migration behavior of all species of birds. Many species probably have similar migration traits. For example, species of warblers wintering in the tropical rain forest in Brazil and migrating to the coniferous forest of Canada probably have similar navigational systems. Although species of sandpipers usually occur in separate flocks, those species migrating from the same tundra area of Canada to the same pampas area of Argentina might reasonably be credited with similar navigational sophistication.

Although this paper is based upon some facts, much assumption, and a great deal of speculation, I believe that it presents a diff-

erent view of previous findings on migration behavior and provides for an orderly approach to future investigations on this subject.

SUMMARY AND CONCLUSIONS

The hypothesis presented in this paper proposes that navigational sophistication evolved as adaptive behavior to expansion of ranges of permanent-resident birds. Other traits being equal, the farther a bird expanded its range, the greater its navigational attributes.

Because birds are basically diurnal animals, the adaptations by many species for nocturnal migration are considered progressive evolutionary development in navigational sophistication. These developments provided long-distance migrants with opportunities to feed diurnally, and provided weak-winged flyers, such as ground-hugging sparrows and rails, with protection from accipitrine hawks.

The landscape is assumed to be the single most important cue for orientation among nonmigratory birds. Therefore, landscape features are considered the most fundamental cues to migrants. The less reliance migratory birds place on landscape for orientation, the more advanced their navigational mechanisms. Therefore, long-ranging pelagic birds are considered to be among those with the most highly developed navigational attributes.

The degree that birds wander from customary migration paths between breeding and wintering grounds is largely unknown. However, a surprisingly high proportion of adult birds return to their previous nesting area. Many juvenile passerines appear to return to areas inhabited immediately prior to their fall migration, accounting at least in part for low returns to their natal areas.

Certain oceanic birds, both adults and juveniles, have an astounding ability to return to nesting islands from thousands of kilometers away. Such homing ability over the trackless sea suggests great navigational sophistication. Sun navigation surely plays an important role among the several environmental cues available to oceanic species.

The ability of many birds to remain oriented when visual cues are minimal is probably one of the more significant findings derived from radar studies. It points to wind structure and/or the Earth's magnetic field as potential sources of directional information. Certainly these are two aspects of navigation that need more investigation.

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COMMON AND SCIENTIFIC NAMES OF BIRDS REFERRED TO IN THIS PAPER

Laysan albatross	*Diomedea immutabilis*
Black-footed albatross	*Diomedea nigripes*
Greater shearwater	*Puffinus gravis*

Manx shearwater	*Puffinus puffinus*
Slender-billed shearwater	*Puffinus tenuirostris*
Giant petrel	*Macronectes giganteus*
Leach's petrel	*Oceanodroma leucorhoa*
Wilson's petrel	*Oceanites oceanicus*
White pelican	*Pelecanus erythrorhynchos*
Gannet	*Morus bassanus*
Brown booby	*Sula leucogaster*
Blue-footed booby	*Sula nebouxii*
Double-crested cormorant	*Phalacrocorax auritus*
Whistling swan	*Olor columbianus*
Canada goose	*Branta canadensis*
White-fronted goose	*Anser albifrons*
Snow goose	*Chen hyperborea*
Mallard	*Anas platyrhynchos*
Florida duck	*Anas fulvigula*
Pintail	*Anas acuta*
Gadwall	*Anas strepera*
Blue-winged teal	*Anas discors*
Cinnamon teal	*Anas cyanoptera*
American widgeon	*Mareca americana*
Shoveler	*Spatula clypeata*
Wood duck	*Aix sponsa*
Black-bellied tree duck	*Dendrocygna autumnalis*
Common goldeneye	*Bucephala clangula*
Common eider	*Somateria mollissima*
King eider	*Somateria spectabilis*
Spectacled eider	*Lampronetta fischeri*
Oldsquaw	*Clangula hyemalis*
Common scoter	*Oidemia nigra*
Surf Scoter	*Melanitta perspicillata*
Turkey vulture	*Cathartes aura*
Black vulture	*Coragyps atratus*
Rough-legged hawk	*Buteo lagopus*
Ferruginous hawk	*Buteo regalis*
Red-tailed hawk	*Buteo jamaicensis*
Red-shouldered hawk	*Buteo lineatus*
Swainson's hawk	*Buteo swainsoni*
Broad-winged hawk	*Buteo platypterus*
Harlan's hawk	*Buteo harlani*
Osprey	*Pandion haliaetus*
Willow ptarmigan	*Lagopus lagopus*
White stork	*Ciconia ciconia*
Common egret	*Casmerodius albus*
Great blue heron	*Ardea herodias*
Whooping crane	*Grus americana*
American coot	*Fulica americana*

Golden plover	*Pluvialis dominica*
Piping plover	*Charadrius melodus*
Killdeer	*Charadrius vociferus*
Long-billed curlew	*Numenius americanus*
Bristle-thighed curlew	*Numenius tahitiensis*
Upland plover	*Bartramia longicauda*
White-rumped sandpiper	*Erolia fuscicollis*
Ivory gull	*Pagophila eburnea*
Ring-billed gull	*Larus delawarensis*
Black-legged kittiwake	*Rissa tridactyla*
Franklin's gull	*Larus pipixcan*
Arctic tern	*Sterna paradisaea*
Common tern	*Sterna hirundo*
Black tern	*Chlidonias niger*
Noddy tern	*Anous stolidus*
Razorbill	*Alca torda*
Common murre	*Uria aalge*
Dovekie	*Plautus alle*
Horned puffin	*Fratercula corniculata*
Whiskered auklet	*Aethia pygmaea*
Homing pigeon	*Columba livia*
Mourning dove	*Zenaidura macroura*
Yellow-billed cuckoo	*Coccyzus americanus*
Black-billed cuckoo	*Coccyzus erythropthalmus*
Snowy owl	*Nyctea scandiaca*
Chimney swift	*Chaetura pelagica*
Yellow-shafted flicker	*Colaptes auratus*
Redheaded woodpecker	*Melanerpes erythrocephalus*
Yellow-bellied sapsucker	*Sphyrapicus varius*
Collared flycatcher	*Muscicapa albicollis*
Horned lark	*Eremophila alpestris*
Barn swallow	*Hirundo rustica*
Cliff swallow	*Petrochelidon pyrrhonota*
Tree swallow	*Iridoprocne bicolor*
Bank swallow	*Riparia riparia*
Purple martin	*Progne subis*
Blue jay	*Cyanocitta cristata*
Gray jay	*Perisoreus canadensis*
Common crow	*Corvus brachyrhynchos*
Black-capped chickadee	*Parus atricapillus*
Red-breasted nuthatch	*Sitta canadensis*
House wren	*Troglodytes aedon*
Bewick's wren	*Thryomanes bewickii*
Mockingbird	*Mimus polyglottos*
Robin	*Turdus migratorius*

Eastern bluebird	*Sialia sialis*
European robin	*Erithacus rubelcula*
Golden-crowned kinglet	*Regulus satrapa*
Bohemian waxwing	*Bombycilla garrulus*
Cedar waxwing	*Bombycilla cedrorum*
Loggerhead shrike	*Lanius ludovicianus*
Starling	*Sturnus vulgaris*
Black-capped vireo	*Vireo atricapilla*
Bay-breasted warbler	*Dendroica castanea*
Blackpoll warbler	*Dendroica striata*
Pine warbler	*Dendroica pinus*
Kirtland's warbler	*Dendroica kirtlandii*
Ovenbird	*Seiurus aurocapillus*
Northern waterthrush	*Seiurus noveboracensis*
Canada warbler	*Wilsonia canadensis*
House sparrow	*Passer domesticus*
European tree sparrow	*Passer montanus*
Bobolink	*Dolichonyx oryzivorus*
Eastern meadowlark	*Sturnella magna*
Red-winged blackbird	*Agelaius phoeniceus*
Brewer's blackbird	*Euphagus cyanocephalus*
Common grackle	*Quiscalus quiscula*
Brown-headed cowbird	*Molothrus ater*
Indigo bunting	*Passerina cyanea*
Evening grosbeak	*Hesperiphona vespertina*
American goldfinch	*Spinus tristis*
Dickcissel	*Spiza americana*
Rufous-sided towhee	*Pipilo erythrophthalmus*
Chaffinch	*Fringilla coelebs*
Field sparrow	*Spizella pusilla*
White-throated sparrow	*Zonotrichia albicollis*
Song sparrow	*Melospiza melodia*
Lapland longspur	*Calcarius lapponicus*

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Topography and Pigeon Orientation*

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A FEW YEARS AGO in Switzerland we started a series of investigations concerning the problem of whether topographical factors influence homing pigeons' orientation. Up to now, the opinions expressed in the literature have been confusing. Some authors (ref. 1) believe that there is no topographical influence at all, whereas others (ref. 2) try to prove that topographical cues alone lead pigeons back to their loft. Kramer (ref. 3) reports a clear influence of the sea coast on the initial orientation behavior of Wilhelmshaven pigeons released from the Danish island of Bornholm. However, it seemed to us that there had not been sufficient experiments conducted specifically to study this question. Most conclusions were drawn from experiments carried out for other purposes.

Switzerland with its high mountain ranges, its valleys and lakes, is a most suitable country for conducting such homing experiments. There is no doubt that the problem is a complex one. It can be divided roughly into two particular problems:

(1) Whether topographical cues influence the initial orientation of the pigeons when released and, if so, how,

(2) Whether topographical cues influence the actual and complete homeward flight and, if so, how.

To study the first problem, pigeons can be released in the conventional manner, one by one and in a statistical number, from places of topographical interest. The pigeons then are observed through binoculars as long as possible. The bearings (azimuth) of each pigeon are noted at 20, 40, and 60 sec after release and plotted on concentric circles. Statistical evaluation follows according to the methods of circular distribution: Do the directions chosen by the pigeons show a uniform distribution? If not, is there any evidence of a topographical influence at that particular point of release?

We call the conventional release method the "ground method." Its disadvantage is that one can only follow the pigeons for the first 2 or 3 km of their flight, but one does not know at all what they will do beyond that.

To study the second problem, that is, the actual way home, pigeons have to be followed directly or indirectly in their flight. Such experiments have been performed by different investigators and with different methods. Griffin and others followed displaced seabirds; Matthews followed displaced

* The maps in this paper are reproduced by permission of the Swiss National Institute for Topography (*Schweizerische Landestopographie*).

pigeons on their homeward flight by means of a normal aircraft. However, a normal aircraft cannot fly as slowly as pigeons and, therefore, must fly in curves and circles. Thus, it becomes very difficult for the observer to keep track of the pigeons. Mitchener and Walcott (ref. 4) introduced the "radiotracking" method of following the pigeons. These investigators were able to trace the complete homing flight for a great number of singly released pigeons. The disadvantage of this method, however, is that the pigeons' behavior during the flight, especially their reactions to topographical structures, cannot be observed in detail.

Tracking pigeons by helicopter avoids the disadvantages of both ground and aircraft tracking. By helicopter one can follow the pigeons at their exact speed and even stay very close to them. Their flying behavior can be observed all the time; and, when they are released in a flock, it is possible to study the flock's behavior. We studied the pigeons' actual way home in this manner, and called this method the "helicopter method."

METHODS

Ground Method

To study the influence of topographical cues on initial orientation, we used the conventional releasing method. The topographic structures chosen were water surfaces and mountain ranges. The releasing points in these experiments were normally selected in such a way that, to take the shortest route to their loft, the pigeons had to cross a lake or a mountain range at the beginning of their flight.

The number of pigeons usually released was 20 or more from one loft, sometimes less. The pigeons necessarily originated from different lofts and cannot be considered as homogeneous. This fact, however, did not seem to be a serious disadvantage. On the contrary, it was interesting to study the reactions of different pigeons to the same topographical factors.

Helicopter Method

To study the complete flight of the pigeons from the releasing point to the loft, we used a French Aloutte III helicopter. Since the Swiss army maintains a homing pigeon service and, therefore, was interested in our investigations, we were granted a military helicopter and a pilot for 10 flying hr in 1969 and for 15 hr in 1970.

In our first flights we worked with flocks of 20 to 30 pigeons. It proved to be quite easy to keep them in view, and the birds were not disturbed by the presence of the aircraft even when followed as close as 30 to 50 m. We released flocks of only five to ten pigeons in the 1970 experiments. Sometimes, when the flock divided into smaller flocks, we could follow only one or two individuals.

During the flight we could not only trace the exact homing route on the map, but also measure the altitude over ground as well as the horizontal and vertical speed.

GROUND-METHOD RELEASES UNDER ALPINE CONDITIONS

When released under alpine conditions, the diagrams of the bearings soon after release show clearly a topographical influence. This influence is demonstrated in the following three examples.

Release Nr. 14/68 [1]

This release in the Toggenburg valley re-

[1] From Wattwie (600 m alt) to Wetzikon: 22 km at 270° az; Sept. 30, 1968; 1126–1530 hr.

sulted in a clear bimodal distribution as shown in figure 1. The bottom of the valley, 600 m above sea level, is about 1 km wide, and the mountain ranges on both sides rise up 1000 to 1300 m within a distance of 2 to 3 km. The home direction includes an angle of 70° with the downward direction of the valley. On both sides, villages of about 5000 inhabitants were visible in the valley axis and at a distance of about 2 km. The sky was completely covered that day by very low clouds with a moderate wind blowing from the southwest.

The pigeons, taken from a loft at Wetzikon, were trained from different directions. They clearly preferred the axis of the valley in both directions. Although the number of pigeons is only 13, the distribution of the vanishing points is obviously not uniform. All the 13 vanishing points are located within the two 90° sectors covering the upward and the downward direction of the valley. Statistical evaluation using the Roa test, (ref. 5) shows that the hypothesis of a uniform distribution can be rejected with an error probability of about 7 percent. Table 1 shows the preference for the two sectors covering the valley's axis immediately after release.

In this case, however, it is possible or even likely that the strong bimodal distribution is due to the location of the two villages in the axis of the valley and not so much to the two mountain ranges. The pigeons' loft was located in a village of similar size. This conjecture is supported by the fact that during the first minute after release, most of the pigeons flew in the direction of the nearest village. At the vanishing point, however, most of them had chosen the opposite sector which was in better agreement with the home direction. We made the same observation in many other releases; i.e., pigeons living in a village are often attracted by the view of other villages.

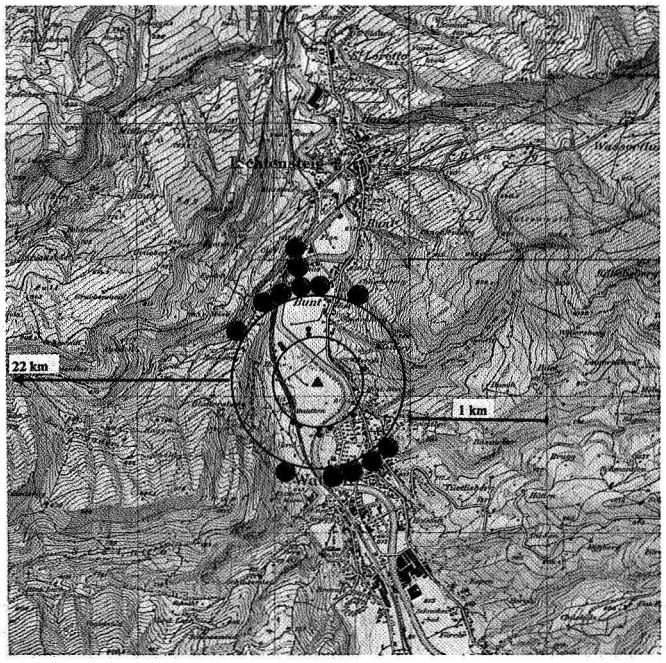

FIGURE 1. Release no. 14/69 in the Toggenburg Valley. Vanishing diagram (● ●) shows a clear bimodal distribution with modes in directions of the valley's axis. The 20-sec diagram (black spots) already reveals a preference for the valley. Home bearing is indicated by arrow.

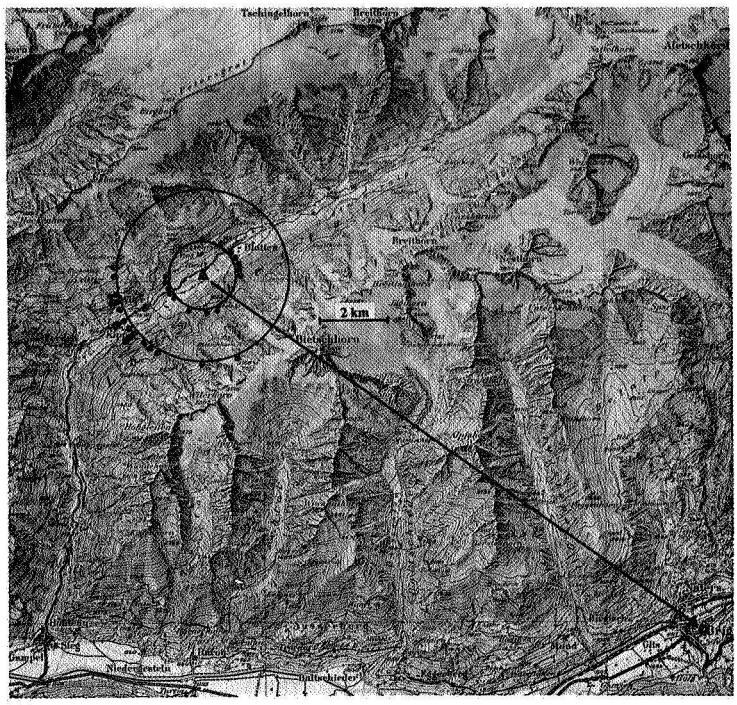

FIGURE 2. Release no. 8/68 in the Loetschental. Bimodal distribution after 20 sec but unimodal "downward" distribution of vanishing points. Home bearing (arrow) hits the Bietschhorn massif (3934 m).

Release Nr. 8/68 [2]

This release (fig. 2) shows a strongly unimodal vanishing distribution. We obtained it in the Loetschental, an alpine valley below the timber line. The releasing point was located at the bottom of the valley, 1450 m above sea level. The valley's bottom was only 500 m wide, and the slopes of both sides ascended up to 3200 m and more within a horizontal distance of only 3 km.

The valley floor had a moderate descent of 5 percent from NE to SW coming down in a straight line from a large glacier. Downward, the valley turned to the left at a distance of 4 km from the releasing point into a very steep and deep gorge, leading out to the main valley of the upper Rhone. The loft was located at Brig in the Rhone valley at a distance of 18 km. The straight line home hit the Bietschhorn, the highest point of the region—nearly 4000 m above sea level. The sky was cloudless that day; all the mountains around were clearly visible. The temperature at the releasing point was 17°C and a moderate wind of 1.5 m per second blew from the southwest.

In this case, the flight directions after 20 sec yielded a clear bimodal distribution with modes in the axis of the valley. However, flight directions into the upward sector (with a view toward the glacier) decreased during the following minute. The vanishing diagram showed a typically unimodal distribution with the mode in the downward direction of the valley.

The bimodal distribution at the beginning as well as the unimodal distribution in the

[2] From Loetschental (1450 m alt) to Brig: 18 km at 125° az; Sept. 24, 1968; 1038–1233 hr.

TABLE 1.—*Distribution of Flight Directions on the Four 90° Sectors in Release Nr. 14/68*

Time from release to bearing check (sec)	N	E	S	W	Total	p(Roa test)
20	4	1	5	1	11	>0.05
40	3	1	6	2	12	>0.05
60	3	1	6	1	11	>0.05
120	1	0	7	0	8	<0.01
V	8	0	5	0	13	>0.05
All values	19	3	29	4	55	<0.01

TABLE 2.—*Distribution of Flight Directions in Release Nr. 8/68*

Time from release to bearing check (sec)	1[a]	2[b]	3[c]	4[b]	Total	p(Roa test)
20	6	2	6	1	15	>0.05
40	5	5	9	2	21	>0.05
60	4	4	8	0	16	>0.05
120	2	2	13	1	18	<0.01
V	0	2	17	1	20	<0.01

[a] 90° sector in the upward valley direction
[b] Sectors rectangular to the valley
[c] 90° sector in the downward valley direction

vanishing points can easily be explained by the topographical situation. The homeward direction does not seem to play an important role in the initial orientation under these conditions. Table 2 shows the distribution on the four sectors and their significance levels after the Roa test.

Release Nr. 9/68 [3]

This release (fig. 3) was performed under high alpine conditions above the snow line. The releasing point was the top of the Langfluh near Saas Fee in the Wallis canton. The Langfluh is a long shaped rock ascending 2500 to 2900 m above sea level. In all directions, except a narrow northeast sector where the tourist center of Saas Fee was visible, there was nothing but snow and ice. The home direction almost coincided with the direction to Saas Fee. The weather during this release was excellent; the temperature was 12°C with a moderate wind blowing from the mountain side (SW). The pigeons used in this experiment had been trained

[3] From Langfluh (2885 m alt) to Brig; 27 km at 17° az; Aug. 25, 1968; 1000–1133 hr.

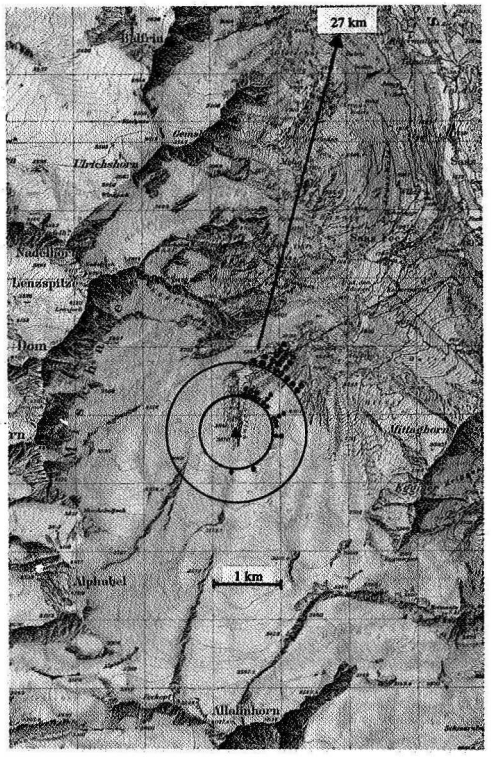

FIGURE 3. Release no. 9/68 from Langfluh (2885 m). Strong unimodal distribution of the 20-sec and the vanishing diagram. Home bearing is indicated by arrow.

within the valleys of the region but not in the high mountains. They were released in 20 groups of two individuals.

The cumulative influence of topography and home direction in this case resulted in a unimodal distribution that was narrower than any we had ever observed before. Forty seconds after release, no pigeon was observed out of a sector of 60°. The 20-sec distribution is also strongly unimodal and far from uniform, although four groups of pigeons had not yet chosen the final direction. The level of significance is already less than 0.01 for the 20-sec distribution. As figure 3 shows, the pigeons left the icy region as soon as possible.

GROUND-METHOD RELEASES FROM LAKES

Water surfaces of relatively small size proved to be as efficient as mountain ranges or snow surfaces in determining the initial bearings.

Release Nr. 1/65 [4]

This experiment was carried out with a small number of homing pigeons from the Swiss Pigeon Service during a military course in 1965 under good weather conditions. It was the first experiment that revealed an evident influence of a lake surface on the direction chosen by the pigeons at the releasing point. The 17 pigeons had been taken from four different lofts, all situated beyond the lake of Neuchatel at a distance of 15 to 25 km. They had a small amount of training that spring but not from this particular direction. Lake Neuchatel has a width of 6 km. We released the birds in groups of two and only measured the vanishing directions.

The diagram shown in figure 4 suggests a preference for the two shore directions (eight and five pigeons, respectively); However, four pigeons disappeared directly across the lake. No pigeon vanished in the opposite direction. Consequently the resulting diagram is trimodal, but statistical evaluation shows that this distribution can be considered as uniform.

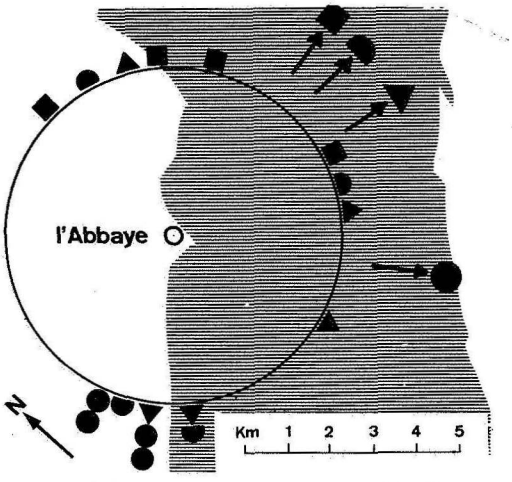

FIGURE 4. Release no. 1/65 from the shore of the Lake of Neuchâtel. Four arrows show (with different symbols) directions of four lofts from which pigeons were taken. Vanishing diagram (circle) is trimodal with two modes in the shore directions and one across the lake.

Release Nr. 21A and 21B/67 [5]

The 22 pigeons used for this experiment (fig. 5) were taken from a loft in Bettwiesen, a small country village 38 to 40 km from the two releasing points. Although they were well selected racing pigeons, they were trained only from the opposite direction.

The release Nr.21A was carried out from Erlenbach, a village located at the right shore

[4] From L'Abbaye to four lofts beyond the Lake of Neuchatel: 15–25 km; May 7, 1965.

[5] (A) From Erlenbach to Bettwiesen: 38 km; and (B) from Horgen to Bettwiesen: 40 km; May 17, 1967.

of Lake Zurich. The experiment was arranged in such a way that, in their home direction, the pigeons had to fly straight away from the Lake.

The vanishing diagram shown in figure 5 reveals that the directions chosen by the pigeons were in good agreement with the home direction within the first 20 sec after release. The length of the mean vector which deviated from the home direction by only 4° was 0.88 ($p<0.01$, Rayleigh Test). Immediately after releasing 16 pigeons from Erlenbach, we crossed the lake by boat with the remaining 12 birds from the same loft, releasing them from Horgen on the opposite side of the lake. Now the directions chosen resulted in quite a different diagram. Soon after release, most of the pigeons chose a direction parallel to the eastern shoreline of the lake. In this case also, the distribution of the vanishing directions is not uniform. The length of the mean vector is 0.64 ($0.01<p<0.05$ Rayleigh Test), but its deviation from the home direction is 79°. The average homing time was distinctly longer than in the Erlenbach experiment. It is possible that most of the pigeons were able to fly around the lake in the time observed for homing.

Release Nr. 3/67 [6]

This release was made from a motor boat in the middle of Lake Konstanz, one of the largest water surfaces in central Europe. The distance from the releasing point to each shore was at least 5 km. The 34 pigeons used were taken from the loft in Bettwiesen. They had limited experience that spring. The weather was hazy, but both shores were clearly visible, the northern shore having better sunlight than the southern; the wind was

[6] From middle of Lake Konstanz to Bettwiesen: 33 km at 247° az; Apr. 3, 1967; 1330–1530 hr.

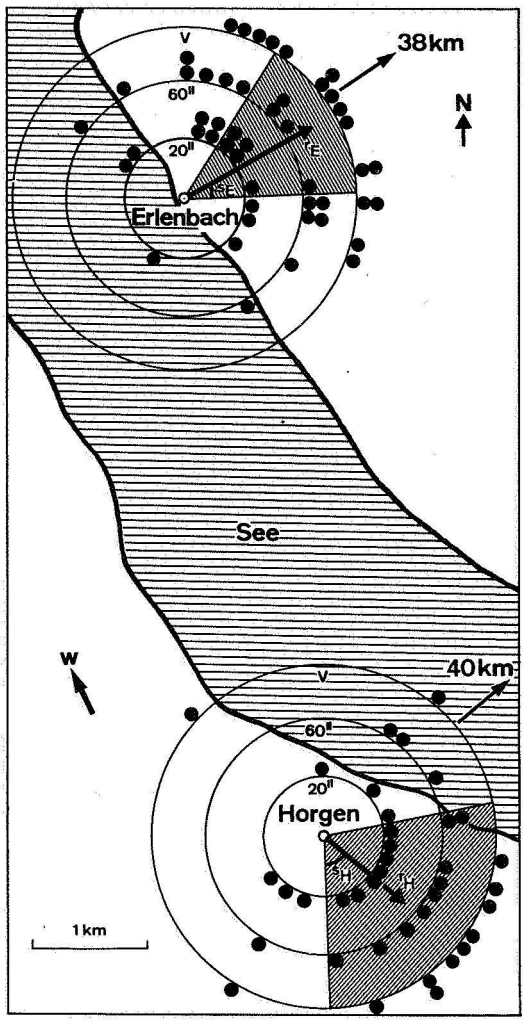

FIGURE 5. Release no. 21A and 21B/67 from the shore of the Lake of Zurich. (A) Release from Erlenbach (*E*) with home bearing away from the lake. (B) Release from Horgen (*H*) with home bearing across the lake. Both diagrams are unimodal (20 sec, 60 sec and (*V*) as well); but in case B the mean vector's (r_H) deviation from the home direction is 79°, and in case *A* (r_E) it is only 4°. The hatched area shows the sector within the mean angular deviation ($s_E = \pm 28°$, $s_H = \pm 49°$). W is wind direction.

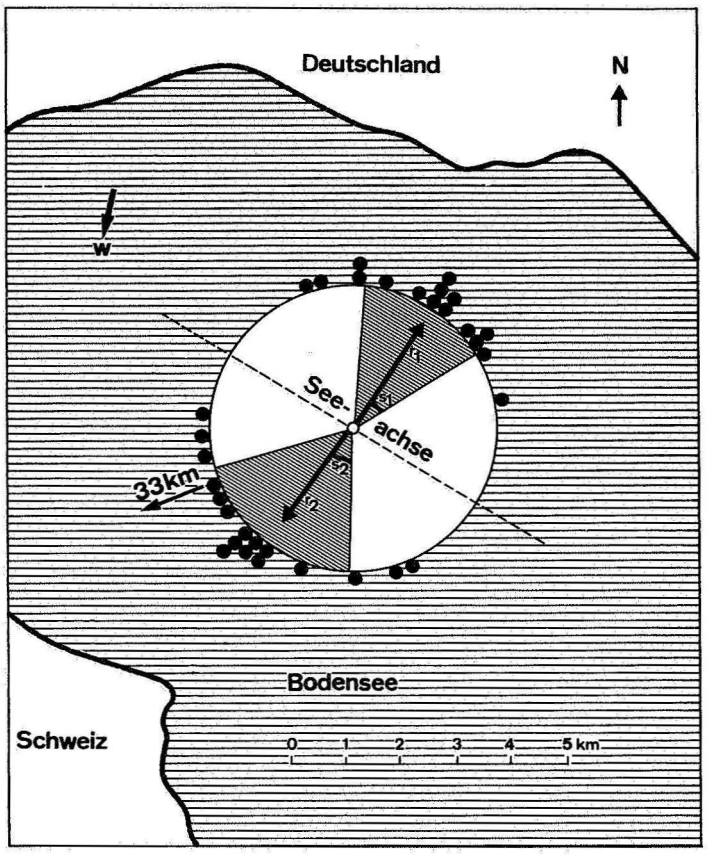

FIGURE 6. Release no. 3/67 from the middle of the Lake of Konstanz. Vanishing diagram is clearly bimodal with modes in the two shore directions. r_1 and r_2 indicate mean vectors of the two groups taken independently; s_1 and s_2, the mean angular deviations ($\pm 26°$ and $\pm 35°$, respectively).

moderate from the north. Immediately after release, the pigeons chose one of the two shore directions. In the first 20 sec, the wrong northern shore was clearly preferred. The vanishing diagram, however, shows a symmetrical bimodal distribution.

Let us consider the northern and the southern groups separately (fig. 6). For each we calculated the mean vector and the mean angular deviation. The length of the mean vectors then are 0.81 and 0.89, respectively. The directions of the two vectors are clearly oriented to the nearest points of the northern and southern lakeshore and seem to be quite independent of the home direction. Both groups show symmetry with respect to their mean vector. The distribution is not uniform with a significance level of $p<0.01$.

The northern group clearly needed more time for homing than the southern one; i.e., 122 min instead of 80 min. Nevertheless, it is likely that some pigeons of the northern group turned to the southern side after having vanished from our binoculars but before reaching the northern shore.

The conclusion of this experiment, as well as of the two experiments related before, is that during the initial orientation (i.e., during the first minutes after release) water surfaces can influence the flight directions to a large extent and eliminate, more or less, the long distance orientation.

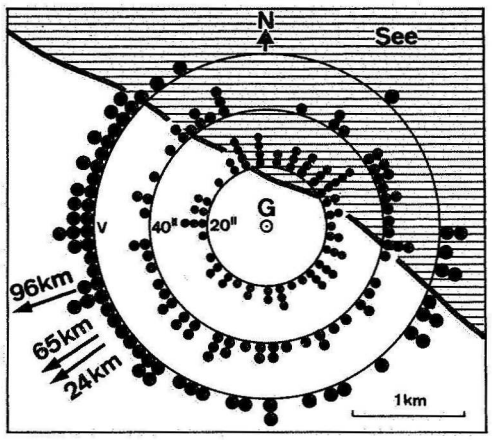

FIGURE 7. Synopsis of all releases from Guettingen (*G*) at the southern shore of the Lake of Konstanz ("See") with home bearings "away from the water." The 20-sec diagram is still uniform. The vanishing (*V*) distribution, however, is unimodal with a "filled" semicircle "land" and a nearly empty semicircle "water." Arrows indicate bearings of three lofts.

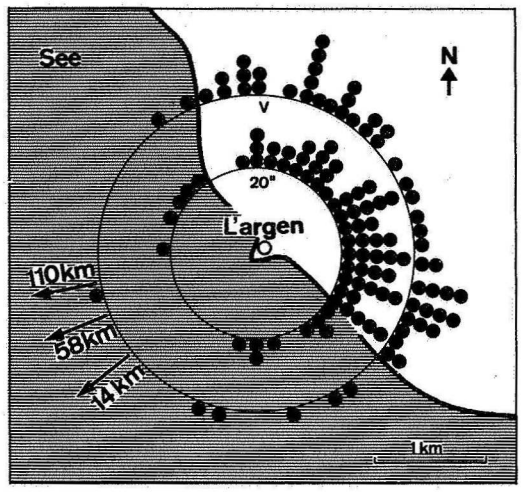

FIGURE 8. Synopsis of all releases from Langenargen (*L*) at the northern shore of the Lake of Konstanz ("See") with home bearings "across the water." Unimodal distribution of the 20-sec and the vanishing diagram (*V*). The "correct" semicircle "water" is empty, and the "wrong" semicircle "land" is filled. The same three lofts (directions indicated by arrows) were used as in the case of figure 7.

Figures 7 and 8 show the influence of the lake surface on a larger statistical basis for the case of shore releases. Figure 7 resumes the bearings of three releases from one point (Guettingen) located at the southern side of Lake Konstanz. Overall, the lofts were situated in about the same direction from the lake but at different distances. The great majority of the vanishing points is situated within the correct semicircle.

Figure 9, on the other hand, summarizes the vanishing bearings of three releases from one point (Langenargen) located on the northern side of Lake Konstanz. The 55 singly released pigeons were taken from the same three lofts as in the three releases from the south side (fig. 7), but this time the home bearings were directed across the lake. The great majority of the vanishing directions is again clearly oriented to the land side, but this is the incorrect semicircle. The two shore directions, however, show clear modes within the semicircular distribution.

HELICOPTER-METHOD RELEASES

What is the pigeon's flight path after vanishing from the view of the ground-observer's binoculars? Do they fly around a large lake? In the mountains, do they follow the valleys and passes to overcome the mountains—or, do our observations, using the ground method, give a wrong impression? To answer this question, we used the helicopter method for extended observations.

In 1969 and 1970 we performed 12 helicopter experiments. In three cases only we could follow the pigeons on their complete flight from the releasing point to the loft. In five cases the pigeons landed before reaching

FIGURE 9. Helicopter track no. 3A/69. *A*, releasing point; *LL*, leading line to the loft (110 km); *L*, landing point after an effective track of 70 km within 60 min.

the loft. In two cases we lost them from view under difficult terrain and weather circumstances (rocks, rainfall). In two other cases we had to quit tracking because of lack of fuel. Nevertheless, the experiments yielded many interesting observations concerning the main question of whether topography does influence the pigeons' orientation behavior. In the following paragraphs we describe two cases of alpine flights.

Helicopter Flight Nr. 3A/69 [7]

This experiment (fig. 9) was performed under good weather conditions with a flock of 27 pigeons trained to home from north. At two critical points the flock divided into smaller flocks. The flock that we followed consisted of 13 pigeons at the end of the flight.

The first 20-km leg of this flight was within the Swiss middleland, a landscape comprised of hills rising not over 1000 m above sea level and valleys lying at 400 to 500 m above sea level. After crossing Lake Zurich, the subalpine level was reached, becoming rougher and rougher with tops over 2000 m. The loft was located within the typically alpine canton of Graubuenden which is in a deep valley. Therefore, the direct homing line crossed many mountain ranges and valleys.

Soon after release, the pigeons chose a direction with a deviation of about 20° to the right of the home direction. This deviation can probably be ascribed to the influence of the training direction. As we had observed in previous experiments, the pigeons generally flew very low over the ground (often within 10 m or less), especially when the ground was ascending. They flew directly toward topographical obstacles such as hills and rocks, turning only at the very last moment and then flying around and not over it. Arriving after 40 km flight in the alpine region, this pattern of behavior implied that the pigeons often followed high vertical rocky walls at a distance of only a few meters. Topographical lines were never followed unless they had the same orientation as the pigeons' actual flight.

Lake Zurich, which had seriously influenced the pigeons' initial orientation in

[7] From Duebendorf to Tiefencastel: 110 km at 138° az; Jul. 17, 1969.

ground-method experiments, was crossed after 20 km of flight. A slight deviation from the course was observed, however, in the sense that the birds chose the shortest way over the water using a small peninsula as a rudimentary "landbridge."

During the first 60 min the pigeons had flown an effective distance of about 70 km. Then they approached a very high rocky mountain range presenting a nearly vertical wall of 700 m height rectangular to the flight direction. In this situation, the pigeons landed near a small mountain lake 1800 m above sea level; i.e., above the timber line in the alpine rubble. We also landed with the helicopter at a distance of about 100 m from the pigeons. They began to preen, then fed between the rocks and probably drank water from a tiny rill.

After 45 min the pigeons did not manifest any intention to continue their flight. We then started our engine and tried to chase them up by approaching the birds very closely with the helicopter, but the downward wind produced by the rotor pressed them to the Earth. We broke off the experiment and flew over to the Engadine valley to start another homing experiment with more pigeons we had on board.

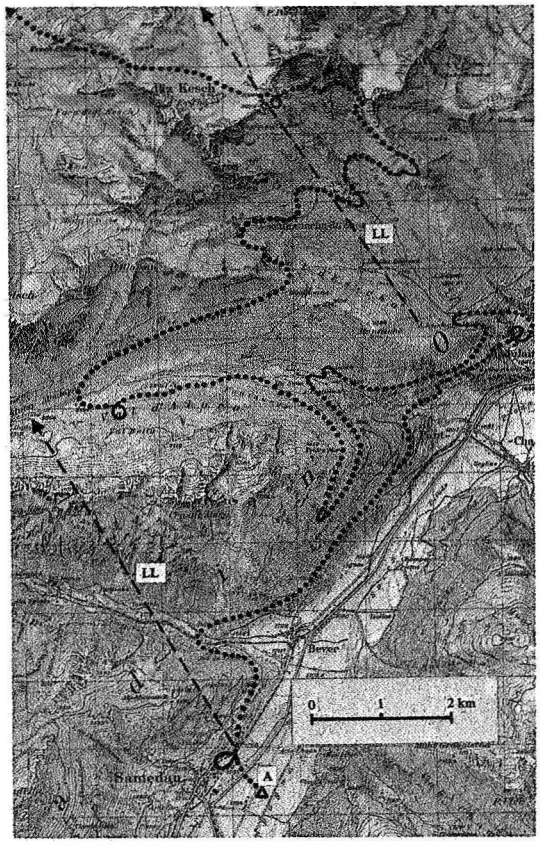

FIGURE 10. Helicopter track no. 3B/69. Track of the first 35 min after release crossing the massif of Piz Kesch (3417.7 m). *A*, releasing point; *LL*, home direction (leading line).

Helicopter Flight Nr. 3B/69 [8]

In this experiment (figs. 10 to 12), the arrangement was opposite that of flight Nr. 3A: The pigeons had to start in the middle of the alps, in the Engadine valley. The straight line to the loft crossed the high alpine massif of Piz Kesch (3421 m). The releasing point was situated at 1700 m above sea level in the bottom of the valley. The 20 birds were taken from the Bettwiesen loft, had good homing experience from different directions, but had never been released from Graubuenden.

The ground experiments previously described suggested that the pigeons would follow the valley's axis in one direction or the other. An Earth observer indeed would have reached the same conclusion in this case. The helicopter method, however, revealed that the pigeons followed the axis of the valley for 8 km only, then turned around and followed the valley's slope in the opposite direction,

[8] From Samaden to Bettwiesen: 125 km at 330° az; Jul. 17, 1969; 1427–1600 hr.

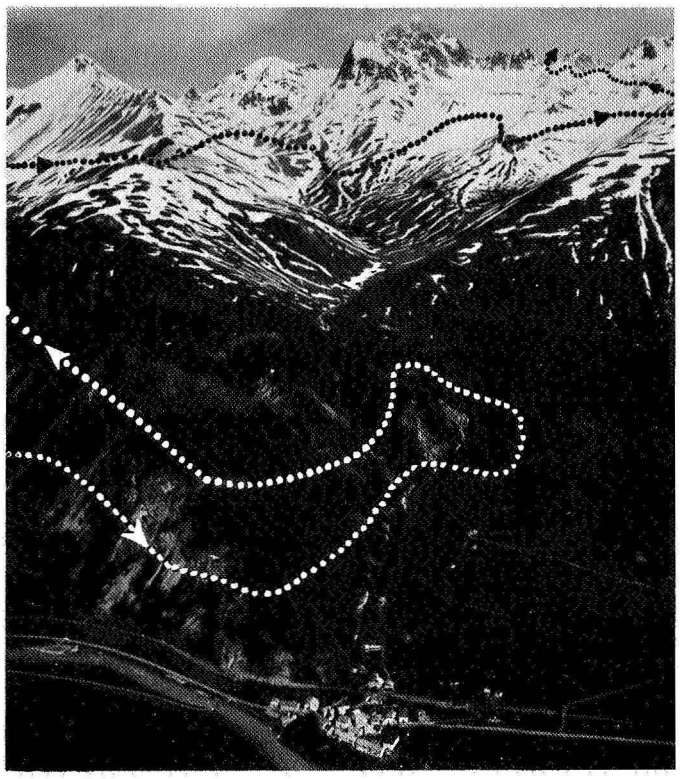

FIGURE 11. Helicopter track no. 3B/69. General view of the Piz Kesch massif from southeast with the pigeons' track.

flying very close to the ground but continually ascending. In this way they reached the Albulapass after having flown different curves and circles. The Albulapass is an important communication line to the Engadine with an alpine road. Having reached the highest point of that pass, the pigeons turned again and approached the massif of Piz Kesch. Following the wild and steep slopes of that massif in constant ascent, they reached a high alpine passage, the Porta d'Escha, 3008 m above sea level and crossed it in good home direction.

After this immense obstacle the rest of the way home presented no problems. Some smaller massifs were crossed in an analogous manner. Several valleys were crossed at 800 to 1000 m above ground. Even the large valley of the Rhine, although leading in approximate home direction, was crossed in direct flight toward the next massif, that of the Calanda (2808 m). This massif, too, was crossed in the typical way.

Unfortunately 20 km later, before the last high rocky barrier on their way home, the pigeons landed at 2000 m in almost vertical rocks near a water rill. It was quite impossible for the helicopter to go down at that point, and we had to terminate the experiment.

In a nonstop flight, the pigeons had covered a distance of 125 km in 93 min, which means their mean speed was 80 km per hour. They had never been more than 7 km away from the shortest line to the loft. Most of them arrived in the loft the same evening.

FIGURE 12. Helicopter track no. 3B/69. *A*, releasing point; *LL*, leading line to the loft (125 km); *L*, landing point of the pigeons after an effective track of 125 km within 93 min.

SUMMARY AND CONCLUSIONS

Two types of homing experiments have been performed with pigeons to study the question of topographical influences on the birds' orientation behavior:

(1) Ground experiments by releasing the pigeons one by one in the conventional manner at points of topographical interest.

(2) Helicopter experiments by following small flocks of pigeons on their homing flight.

The ground experiments clearly revealed a strong influence of topographical factors on the initial orientation; i.e., during the first minutes of flight:

(1) When released at lake shores with home direction across the lake, pigeons generally avoided the water surface.

(2) When released in valleys between mountain ranges, the pigeons preferred the valley axis.

(3) When released in the neighborhood of alpine snow and ice, pigeons avoided flying over the snow.

(4) When released in the neighborhood of a village, the village often attracted pigeons originating from another village.

The helicopter experiments, however, proved that the observations from the ground experiments do not allow conclusions concerning the actual homing way of the pigeons:

(1) Lakes as well as mountain ranges did not affect the general flight direction once the pigeons had recognized the approximate home bearing; both were crossed, if necessary, directly. Never did the pigeons follow a topographic leading line for a long time.

(2) A local influence of topographical factors could sometimes be observed during the homing flight. Mountain massifs can oblige the pigeons to fly many curves and circles to get over the obstacles. Topographic structures that are familiar to the pigeons from home range, e.g., villages or woody hills, can attract the pigeons temporarily and sometimes in a persistent manner. Water surfaces of 2 to 3 km width were of small influence once the pigeons were flying in the proper direction.

In summation, our experiments under Swiss conditions yielded the following results. It is true that topographical factors may influence pigeons' homing behavior in many ways. However, such factors always make homing more difficult and not easier. There are no topographical structures or lines that lead pigeons home. Their long distance orientation system is not affected by topography.

DISCUSSION

QUESTION: Did all of the birds return home?

WAGNER: In the described experiments we used a total of 182 pigeons; 162 of them (90 percent) returned the day of release, 16 the following day. Only three were lost, two in the release Nr. 3A/69 and one in the release Nr. 3/67.

GRIFFIN: Would you give us some information concerning cases when pigeons flew through cumulus clouds?

WAGNER: We performed one experiment in the Alps on a very cloudy day when a thunderstorm was starting. The pigeons had very bad orientation that day. They did fly into a large cumulus cloud once but only for a short time.

WILLIAMS: Did you have any chance to observe pigeons when the sky was totally overcast and the Sun was hidden from view?

WAGNER: Not with the helicopter method, but with the ground method. We obtained well-oriented vanishing diagrams even under complete overcast.

QUESTION: Do two pigeons released at the same time vanish in the same direction?

WAGNER: Generally they fly together and as a consequence vanish together. When released in a flock, the flock will also stay together.

WALCOTT: Did you see any effect of the helicopter on the behavior of the pigeons? Was the homing time of the pigeons who were followed roughly comparable with the pigeons who were not followed?

WAGNER: The homing time in the helicopter experiments was quite normal. We could see a disturbing influence of the helicopter only when we came within 10 to 15 m of the pigeons.

GAUTHREAUX: Did you ever think that you had a steering effect when you were following the pigeons with the helicopter?

WAGNER: No. I think this possibility can be excluded.

GAUTHREAUX: Did the helicopter take off simultaneously with the pigeons as they were released?

WAGNER: The helicopter is waiting in the air when the pigeons are released. After their normal initial circles, we follow them. For technical reasons it is not possible to start with the helicopter after the pigeons have been released.

GRIFFIN: In what position was the helicopter flown relative to the pigeons—behind them or above them?

WAGNER: Behind them; sometimes above, sometimes beneath. It was best to fly slightly beneath them.

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New Experiments on the Effect of Clock Shifts on Homing in Pigeons

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THIS SYMPOSIUM may be considered a successor to the Cold Spring Harbor Symposium of 1960. I, therefore, decided to report on experiments that are extensions of those reported at the previous symposium (ref. 1) even though I have not yet completed them (these data were also included in a preliminary report with limited circulation).[1] More experiments are being carried out at the present time.

Clock shifts have, so far, been the only experimental tools to predictably interfere with homing. Clock shifts introduce specific errors in the birds' Sun azimuth compass (refs. 1 to 3) resulting in corresponding errors during initial orientation and, probably, also during orientation enroute.

In previous experiments, the effect of shifts of 6 hr and of 12 hr has been investigated in releases from 2 km up to 170 km distance, mostly from distances between 12 km and 70 km (refs. 1, 3, and 4). Upon 6-hr clock shifts, the initial orientation of experimental birds deviated roughly 90° from that of the controls and roughly 180° upon 12-hr clock shifts, as would be expected theoretically. However, this was true only on the average: There were considerable and unexplained deviations from the expected values at various individual release sites.

During the past 8 years we have extended these investigations in Germany and the U.S. with particular emphasis on the following questions:

(1) Is the deviation accomplished by the clock shift influenced by the distance of release?

(2) Would smaller degrees of clock shift produce correspondingly smaller deviations?

The same methods were used as previously (e.g., ref. 4) with one major exception: Only well-experienced pigeons (as, e.g., in refs. 5 and 6) participated in these releases. About one-half of the planned total of releases has been carried out to date. A successful shifting experiment involving 6 or more hr of shift, unfortunately, means partial or complete loss of the experimental birds, a

[1] SCHMIDT-KOENIG, K.: Weitere Versuche, durch Verstellen der inneren Uhr in den Heimkehrprozess de Brieftaube einzugreifen. Verh. Dt. Zool. Ges. Würzburg: 1970, pp. 243–245.

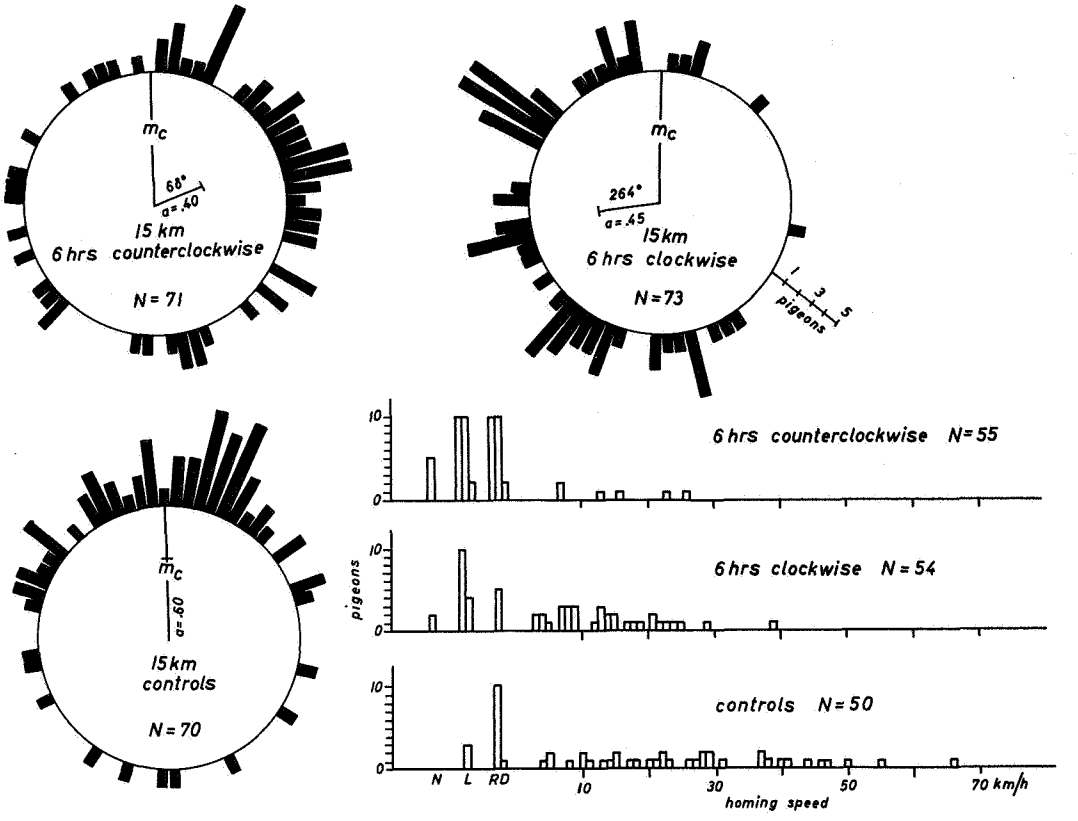

FIGURE 1. Initial orientation (circular diagrams) and homing performance of control and experimental birds from 6-hr shifts clockwise and counterclockwise from 15 km N, E, S, and W at Durham, N.C. From each site, controls and both groups of experimentals were released on the same day. Lengths of bars indicate number of birds according to scale given. Initial orientation of experimentals is plotted with reference to combined mean of controls (m_c). Direction (in deg) and length (a) of mean vectors are given along with sample size (N). N of initial orientation and of homing performance is different because homing performance was not recorded in one of the four experiments.

group of well trained "veterans." Experiments of this kind are, therefore, extremely expensive and time consuming.

DISTANCE OF RELEASE

According to recent findings from North Carolina and Germany (refs. 5 and 6) supported by the results of other investigations (ref. 7)[2] the accuracy of initial orientation of normal pigeons is a function of their distance from home. One possible interpretation of these results is the assumption of the operation of two navigation mechanisms one operating over short distances (up to about 20 km) and the other over long distances (beyond about 100 km). Therefore, we

[2] Also, SONNBERG, A., AND SCHMIDT-KOENIG, K.: Zur Auslese qualifizierter Brieftauben durch Übungsflüge. Z. Tierpsychol., vol. 27, 1970, pp. 622–625.

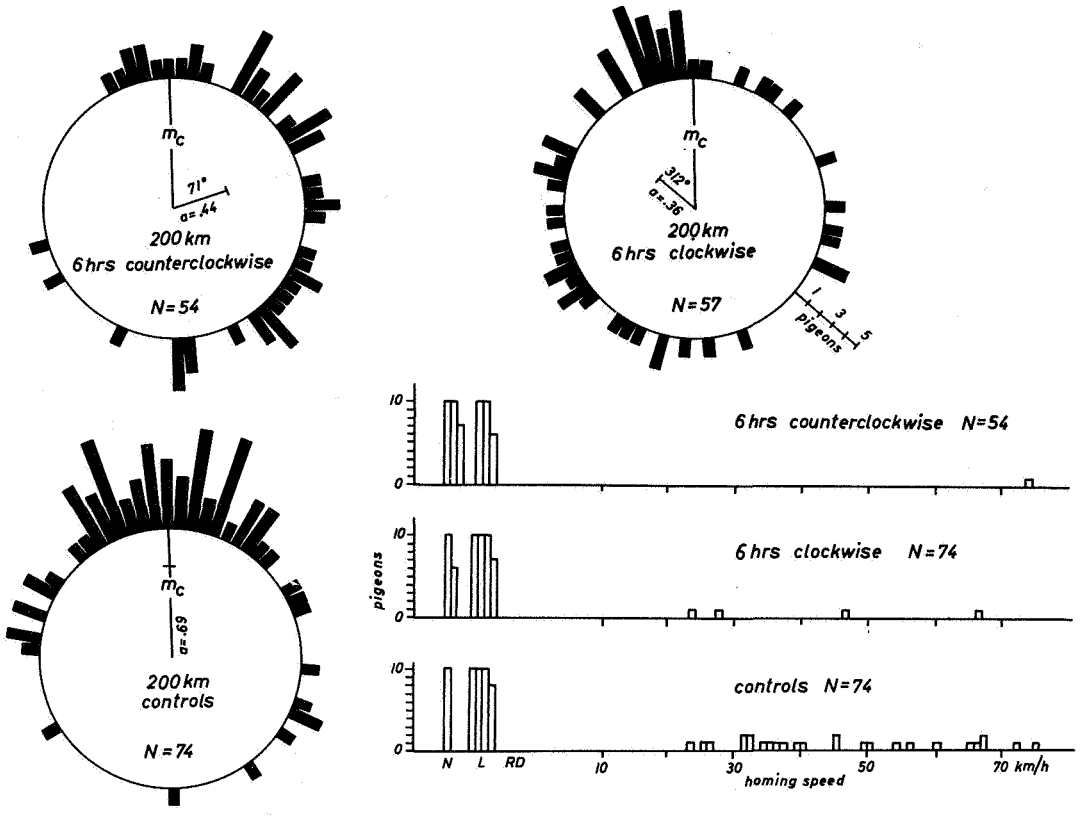

FIGURE 2. As figure 1; however, from 200 km N, E, S, W to Durham, N.C.

sought to discover whether clock shifts would act differently on short-distance and on long-distance releases. In other words, we wanted to find out whether the two hypothetical navigation mechanisms may differ in operating with or without clock and compass. Clock shifts of 6 hr clockwise and counterclockwise (imposed for at least 4 days) were used in a series of releases from 15 km and from 200 km from the cardinal compass directions.

Figures 1 and 2 give the data for initial orientation and homing performance so far accumulated. The following preliminary results may be taken from figures 1 and 2.

(1) The observed deviation confirms previous evidence: the initial orientation was shifted by roughly 90° clockwise or counterclockwise depending upon the sign of the clock shift. Homing performance of the shifted birds was clearly inferior to that of the controls. All differences are significant ($p<0.01$; Watson test, refs 8 and 9; and Mann-Whitney U-test, e.g. ref. 10).

(2) There was no significant difference between the results from 15 km and 200 km.

These data give a preliminary indication that the Sun compass is in fact utilized in short-distance releases as well as in long-distance releases. Thus, if there were, indeed, two navigation mechanisms, they do not seem to differ in this respect.

SMALL CLOCK SHIFTS

Shifts of 2 hr and of 30 min counterclockwise (imposed for at least 4 days) where chosen in another series of experiments. If the Sun is used as a compass, a 2-hr shift can be expected to produce a deviation of about 30° in initial orientation and, perhaps, slightly inferior homing performance (especially on long distances) as compared with controls. In view of the large scatter usually encountered in experiments of this kind, small differences like these cannot be expected to reach significance, certainly not in small samples. Correspondingly, a 30-min shift should produce a deviation of about 8° in initial orientation, thus a measurable difference in initial orientation and homing performance cannot be expected. If, however, the Sun were used for navigation as, for example, suggested by Matthews (ref. 11), a 2-hr clock shift should be interpreted by the bird as a longitudinal displacement of rougly 2000 km (depending upon latitude) and a 30-min clock shift should be interpreted as a longitudinal displacement of roughly 700 km (depending upon latitude). The shifted bird consequently should head east upon a counterclockwise clock shift. Thus, we may expect clearcut results: Little or no appreciable differences should occur in the case of Sun compass orientation, but drastic differences in initial orientation and homing performance in the case of Sun navigation, especially if the direction of displacement is E or S as was the case here.

Figure 3 gives the data of initial orientation and homing performance so far accumulated upon clock shifts of 2 hr counterclockwise. There is no significant difference between the initial orientation of experimentals and controls (Watson test). Homing per-

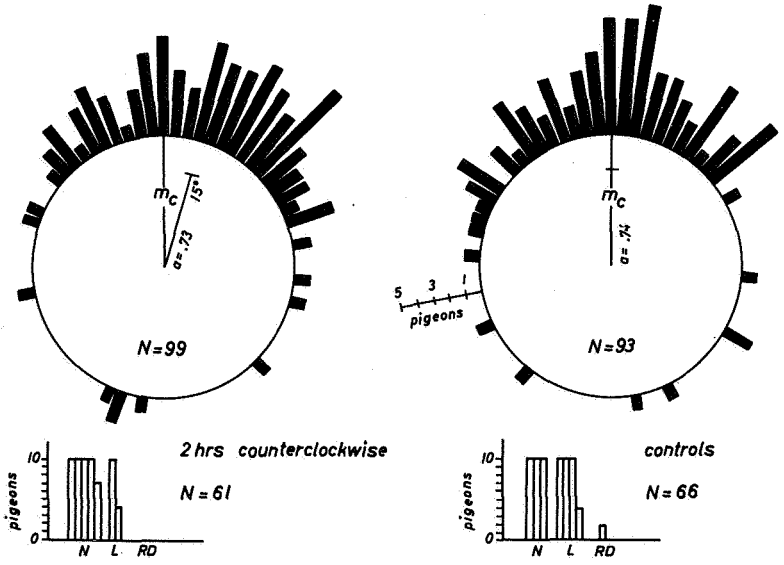

FIGURE 3. Initial orientation (circular diagrams) and homing performance (rectangular diagrams) of control birds and of experimental birds upon 2-hr shifts counterclockwise from 460 and 320 km S and from 280 km E to Wilhelmshaven, Osnabrück, Germany, and Durham, N. C. Symbols as in figure 1.

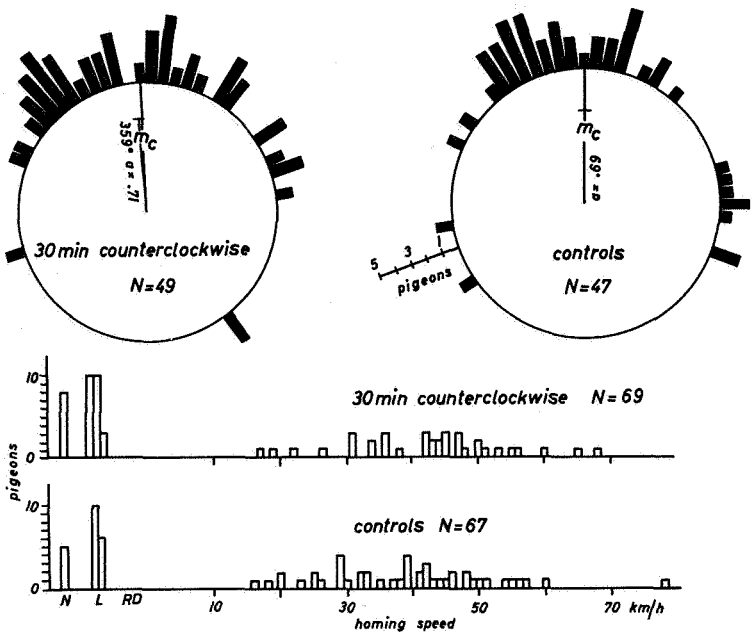

FIGURE 4. Initial orientation (circular diagrams) and homing performance (rectangular diagrams) of control birds and of experimental birds upon 30-min shifts counterclockwise from 130 km S, W, N and 200 km E to Durham, N.C. Symbols as in figure 1. Initial orientation of controls and experimentals at 130 km W was at random; these data had, therefore, to be omitted from the circular diagrams.

formance of controls and experimentals was, however, significantly different ($p<0.01$; χ^2 test).

Figure 4 presents the corresponding data upon clock shifts 30 min counterclockwise. There was no significant difference in either initial orientation or homing performance.

These results clearly support and considerably strengthen previous evidence that the Sun is used for compass orientation and not for navigation. This holds for short distances as well as for long distances. The results from 15 km demonstrate once more that even very experienced birds are easily misled not very far from the loft, indicating that possible knowledge of local factors cannot be very essential to homing.

ACKNOWLEDGMENTS

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DISCUSSION

GRIFFIN: How well were the controls oriented toward home?

SCHMIDT-KOENIG: After we knew that initial orientation is a function of the distance of release, those distances were selected which gave rather

well homewardly directed initial orientation, 15 km and 130 or more km. Thus, the controls were rather well homewardly directed.

QUESTION: Can you conceive of a clock flexible enough to be used as a compass clock and also being stiff enough to be used as a longitude clock?

SCHMIDT-KOENIG: No. A clock for navigation would have to be rather rigid.

WILLIAMS: Was there any methodological rationale for not using similar release points in your various shifts? You took 2-hr shifts between 200 and 450 km and a 30-min shift between 130 and 200 km. This might introduce a new variable.

SCHMIDT-KOENIG: That's correct. These experiments extended over eight years. In Germany the only long distance is to the south. These experiments were done in 1961. Since then, we have become much more sophisticated. We are now using the same release sites for all experiments. However, if you want to generalize these results, they must work at any release site.

ENRIGHT: Are these symmetrical release sites? Were the numbers of releases then balanced in all directions?

SCHMIDT-KOENIG: The 2-hr shifts were not balanced but the others were. The 2-hr shifts were from the south and from the east. There were no north releases and none from the west. Since you would expect the birds to head east, releases from the south and from the east should give you a very clear-cut result if the Sun is used for navigation.

EVANS: In the 2-hr shift experiments, some birds seemed to go off in the same direction as the controls. Did these (experimental) birds have faster homing speeds than those which showed a shift of initial orientation?

SCHMIDT-KOENIG: It is a matter of argument whether or not there is a general correlation between the direction of initial orientation related to homing and homing speed. The long distance releases were very long distances and I don't think that you can get a correlation.

BALDWIN: Can you describe the method of time shifting that you used?

SCHMIDT-KOENIG: The birds are placed in a closed room which is well ventilated and operated automatically on timers. You just reset the timer by as many hours as you want. Since a 6-hr shift takes four days to be completed, all birds were subjected to four days of shifting, even the 30-min birds. The controls are locked up in artificial conditions with no shift. Thus, the only difference is the phase difference in the illumination of the birds.

COCHRAN: In your experiments involving 30-min and 2-hr clock shifts to test navigation, did you have a program where you released the birds at sunrise, at noon and in the evening?

SCHMIDT-KOENIG: The time of day in which you have to release your experimental birds is determined by the clock shift. You have to have the light period which is common for the experimentals and the controls. For birds shifted 6 hr clockwise it is the forenoon; for birds shifted 6 hr counterclockwise it is the afternoon, and for birds shifted 12 hr it is a few hours early in the morning and a few hours late in the evening, in which the artificial day and the natural day overlap. Thus, you are restricted to a certain time of day for the release. Otherwise, you would release your experimental birds in the real day but their personal night. This poses problems of a different sort.

ENRIGHT: What happens when you do release them at night?

SCHMIDT-KOENIG: You get a large scatter. There is some indication that the pigeons (as was demonstrated in stationary training experiments) unlike bees, "think" that the Sun goes counterclockwise at night. We roughly got the corresponding departure directions. We discontinued these experiments because they don't lead very far.

KEETON: We have not yet tracked birds by airplane when they have been clock-shifted, but we have tracked them by radio from the ground. The birds in a 6-hr shift head off roughly 90° wrong. They are still going in that wrong direction when we lose them at about 16 km.

SCHMIDT-KOENIG: We have one more point of evidence. In Germany we have a contrast to the situation in North Carolina. We get many reports of birds that do not home; the direction of the reports roughly agrees with the takeoff direction of shifted birds only for those reports made during the release day or the next day. If more days had elapsed between release and report, then the relation deteriorates very rapidly.

ADLER: You released your birds close to the distances you had previously identified as the "dead belt" (ref. 5). Did you do anything more on exploring whether this effect is true or not?

SCHMIDT-KOENIG: I repeated the North Carolina experiment in Germany. The results from Durham were confirmed in Western Germany with one major or minor exception, the reason for which I don't yet know. The initial orientation again deteriorates beyond 200 km; at 300 km it is particularly bad. I don't know how regular this is going to con-

tinue if you extend releasing to 400, 500 and 600 km.

KEETON: We have now completed nearly 175 releases involving approximately 2550 birds and do not find a distance effect. We have also done clock-shift tests at 32, 48, 64, and 80 km and obtain precisely the same kind of results as at longer distances. We have also done a series of tests at even shorter distances of about 2 km. As long as they cannot see the loft directly the birds appear to be still going off in the wrong direction. If they can see the loft they head straight for it, as Graue has also found.

SCHMIDT-KOENIG: I have done a number of releases in Wilhelmshaven, Germany about 2 km away from the loft. Although they could see the loft very well many experimentals headed away from the loft. Some were recaptured in Ruhrgebiet which is 250 km away.

KEETON: Wondering what information the birds might be getting from the Sun, we conducted this summer a series of tests in which birds being shifted were permitted to go out into an aviary and see the Sun during the overlap period between their shifted day and the true day. When those birds were tested at the end of about five days, they were just as well shifted as ones that had been in a completely light-tight room. Apparently as long as they are just sitting in the aviary it doesn't matter whether they can see the Sun; the only information they appear to obtain from the Sun under such circumstances is whether the lights are on or off.

SCHMIDT-KOENIG: Right. Our evidence is not as sophisticated but if we kept the birds uncovered before the release at the release site for, let us say 2 hr or so, there was absolutely no impact on the shifting effect.

KEETON: I might mention a more confusing thing, although it may not hold up when more tests are conducted. During the overlap period between the true day and the shifted day some birds were permitted to go out and exercise, that is, fly over the loft. When these birds were tested at the end of the proper number of days, they went random (in three tests so far). In other words, if they just sit in the aviary and see the Sun, pigeons are shifted effectively and go non-randomly at the predicted wrong angle from home when tested, but if they are permitted to fly during the overlap periods while being reset, they appear to become confused and do not orient when tested. I emphasize again, however, that these are very preliminary results.

SCHMIDT-KOENIG: That all agrees quite well with what we have found, but there is a disagreement between your finding and my finding of this initial orientation and distance relation. I am very curious what the basis for this may be.

You also find an effect of overcast on shifting. We did not find it with rather small samples, however. I understand that Ithaca, N. Y., has a long period of solid overcast, which we don't have, even if the well-known bad climate of Germany is considered. If you look for solid overcast you just don't find it. That may be the reason for the difference.

KEETON: We find, just as you do, that if we test birds without previous experience under overcast they go random. If, however, the birds have been given a series of 4.8 to 16 km training flights under overcast, they can then be jumped to 160 or 240 km and will orient under overcast. It is essential for the birds to have had some prior short-distance experience under overcast before they are tested at these longer distances. It is certainly true that in Ithaca our birds experience solid overcast much of the time during the autumn months.

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The Navigation of Homing Pigeons: Do They Use Sun Navigation?

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MANY INVESTIGATORS have followed flocks of homing pigeons as they returned to their home lofts from distant release points (refs. 1 to 6). Yet the track made by a flock of pigeons represents some unknown concensus among the pigeons making up the flock. It could well be that different pigeons use different navigational strategies and that the study of flock behavior would reveal very little about any individual pigeon's technique for finding its loft. For this reason my colleagues and I have spent the past 5 years mapping the tracks of individual homing pigeons as they returned to their lofts. Our hope was that a detailed knowledge of what a pigeon did on its homeward journey might provide some clues to its navigational scheme. In addition we hoped that the effect of our experimental manipulations would be seen more clearly by examining the pigeons' tracks than were revealed in either the initial headings or the overall homing performance.

In this paper I will summarize the results of our analysis of the pigeon's tracks, the effects of short clock shifts, the effects of attempts to disrupt the pigeon's internal clock with heavy water, the transporting of pigeons to the release site under anesthesia, and the effects of placing small magnetic fields around the pigeon's head.

TRACKS

In following individual pigeons returning home from release sites where they had never been released before, their tracks could often be divided into three phases; an initial flight in the compass direction in which the bird had been trained, a segment of track directed toward the loft, and a final turn toward the loft itself. We have called these three phases: compass orientation, true navigation, and landmark orientation. Each will be briefly described below.

Many of the pigeons from the loft at Harvard University in Cambridge, Massachusetts, flew east in their trained compass direction when released from a point off their training line. That this was not simply a tendency to fly in an easterly direction was shown by pigeons that had been trained from other directions—from the north and south; they also would frequently fly for 5 or 10 mi in their trained direction when released at unfamiliar locations. But this compass orientation has become less common in recent years, and the

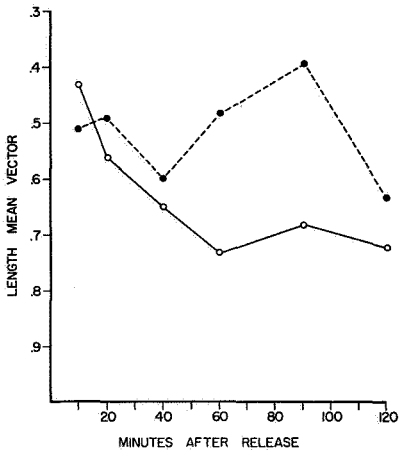

FIGURE 1. Accuracy of homeward orientation of pigeons released off their training line plotted against time after release. Data were derived from tracks of 48 pigeons released at various new release points in different directions from the loft. Bottom solid line represents scatter of homeward bearings measured from release point and graphed as length of mean vector of distribution. Gradual downward slope of the curve simply means that birds flying incorrect courses tend to correct them with time. This distribution also shows a downward trend because as birds fly away from the release point, the angular error to the home loft as measured from the release point tends to decrease. To compensate for this distortion, we have plotted in the upper dashed curve, the mean orientation of 1-mi segments of tract at the specified times. Thus a bird that initially headed away from the release point in the wrong direction would contribute to large scatter in both curves at the outset. As it corrected its course toward the loft, error in its 1-mi track segment might well drop to zero, but its bearing from the release point might still show an error of as much as 180°.

birds in the Lincoln loft rarely show it. One can speculate that this difference may be the result of less extensive training in one direction: the Harvard birds had nearly 30 releases along the training line; the Lincoln birds rarely have more than five or 10 releases in any one direction. Furthermore there is a great variation fom one bird to another in their tendency to fly in the trained compass direction. Some birds often show this behavior often while others almost never do.

But flying in the trained compass direction will not get a bird home if it is released off its training line. And we find that the vast majority of our pigeons do home successfully. In fact our birds are able to orient toward the loft from what is almost surely unfamiliar territory. Several pigeons have shown accurate orientation toward the loft from over the open ocean, well out of sight of land. Furthermore, those birds that don't fly in the trained compass direction orient toward the loft quite rapidly. As figure 1 shows, the tracks show only a gradual decrease in scatter from 10 to 50 min after release. In fact, lumping all off-training line releases from all release points together and plotting the 16-km bearings relative to the homeward direction (fig. 2) reveals that the 16-km bearings are quite tightly grouped with a mean vector differing from the home direction by only a few degrees.

In the last stage of homing when the pigeon arrives in the area near the loft, it appears likely that it uses landmarks to find the loft itself. For birds returning to the loft at Harvard University in Cambridge, it appeared that they made a final course correc-

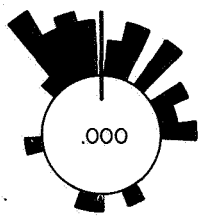

FIGURE 2. 10-mi bearings of 35 birds released from new release points. Bearings are plotted relative to home direction indicated by the line. Number in center is probability that observed distribution is due to chance.

tion when they came within sight of some of the high Harvard buildings—a pigeon flying at tree-top level should have been able to see the buildings when it was about 8 to 16 km (5 to 10 mi) from the loft and indeed most of the pigeons made final course changes within a few km after passing this 8- to 16-km point. (See ref. 7, p. 113 and ref. 8, p. 316 for diagrams.)

It is also possible that landmarks play other roles in the homing process. There is a suggestion from some tracks that landmarks are used as check points by pigeons returning from familiar release points. (See, for example, fig. 4 in ref. 8). But pigeons flying incorrect courses toward the loft do not seem to correct them even when flying through territory that they have flown over many times before (ref. 7, p. 124). It appears then that under sunny conditions, landmarks play only a minor role in homing. But when the Sun was not visible, three pigeons appeared to use landmarks to find the loft. These birds when released along their training line followed a major highway from the release point to the loft. Under sunny conditions their tracks instead of following the highway went straight home.

Pigeons probably use a variety of cues in their homing, and it is a mistake to think that any one single system is totally relied upon. In our years of following individual pigeons, we have been continually impressed with the variation in strategy from one pigeon to another. For example, Blue 77, one of our oldest birds, has been flying for 5 yr. And no matter what experimental regime we subject her to, she always flies straight home, on some occasions with a great deal of sitting. And once when something went wrong with her transmitter harness, she was found slowly walking down a major highway toward the loft.

Another bird, WY, was trained from Orange, Massachusetts, 83 km (52 mi) west of the loft. On the way home all birds from Orange flew past Mt. Wachusett, a conspicuous but not very high mountain, directly on the route home. After training on this line, wherever WY was released the first thing it did was to fly toward the nearest mountain, whether it was Mt. Wachusett, Mt. Monadnock, or Mt. Washington. After circling the mountain, it generally turned and flew directly toward the loft. The final and perhaps the most unusual example was B38 who always navigated very accurately towards the loft. But when it arrived in the region of the loft, it seemed unable to find home. On four of its last five flights, B38 flew past the loft, missing it by only 1 to 2 km and continuing past it for 5 to 16 km (3 to 10 mi). It then landed in the front yard of a house and would allow itself to be captured. The finder then read the label on its transmitter, telephoned the loft, and B38 would arrive home in a taxi. This was a rather unusual strategy but none the less effective.

The moral of these stories is that there is probably a variety of techniques and strategies that pigeons use to find their lofts and that unless the investigator is aware of this diversity, experiments in which pigeons are deprived of one source of information may simply lead the bird to switch to alternate strategies. One of the major advantages of working with individual pigeons is that one can become familiar with the tactics a particular pigeon is most likely to use. Then when one does an experiment, it is easier to assess whether the experimental treatment has had any effect.

During our early tracking, we were impressed with how reluctant our pigeons were to fly if the Sun was not visible. Pigeons flying courses toward the loft would frequently stop and sit when the Sun became obscured; still other pigeons would refuse to

fly at all if the Sun were not visible. Only after extensive training under overcast could we presuade our pigeons to home successfully without the Sun. These observations led us to wonder if perhaps the pigeons were not only using the Sun as a compass, but also as the basis of their navigation, as Matthews (ref. 9) suggested. But the evidence for Matthews' theory and for Pennycuicks' (ref. 10) modification of it rests on two sorts of experiments: clock shifts on the one hand and the confinement of birds during the autumnal equinox on the other. A repetition of the crucial experiments by other investigators has yielded different results (refs. 11 to 16). It could be argued that pigeons using Sun navigation exposed to 3- or 6-hr clock shift would simply not "believe" the amount of displacement that such a shift would indicate (ref. 17). For example, a 3-hr shift is equivalent to moving several thousand km on the surface of the Earth, and for pigeons trained to fly only a few hundred km, such a shift might conceivably be ignored.

What we sought to do was to expose pigeons to very small clock shifts of only a few minutes, small enough to lead to only a trivial error in their Sun compass but to a relatively-easy-to-assay error in their navigation. For example, a 5- or 10-min clock shift would generally lead to only a 2° to 3° error in a Sun compass but in terms of Sun navigation would be equivalent to a displacement of 80 to 160 km (50 to 100 mi). These experiments were performed by confining pigeons, whose normal homing performance was known, to clock shift boxes. These boxes were equpped with artificial lights and timers arranged to turn the lights on and off the appropriate number of minutes either before or after local sunrise or sunset. Details of the procedure and results are given in reference 8.[1] Pigeons were exposed to "0" shifts (lights on at local sunrise and off at local sunset) and to shifts of 5, 10, 15 to 20, and 120 min. The birds were then equipped with radio beacons and taken in covered containers to release points where they had never been before and released. They were tracked by airplane and by ground tracking stations. Figure 3 shows the bearings of each bird relative to the home loft when it was 16 km (10 mi) from the release point, as well as its bearing plotted relative to the "false home," i.e., that location where the local time agrees with the shifted time imposed on the pigeons.

It is obvious from the figure that there is no consistent orientation toward the false home nor is there any significant difference in the accuracy of the homeward orientation of the different shifts. There is, however, an interesting change in the mean vector of the birds given various shifts; the mean vector moves from left to right as one looks at controls, 0 shift, 5-min, 10-min, 15- to 20-min, and 120-min shifts.

An examination of the longer shifts, namely 120 min and 6 hours, shows that the 120-min birds are deviating to the right of the homeward direction. Applying a correction for the Sun-azimuth change involved in the 2-hr shift gives a distribution (fig. 4) that is much closer to the true homeward direction. The 6-hr shifts are really too scattered to analyze and the fact that we lost three of the five birds made us reluctant to increase the sample.

The results suggest that small clock shifts have little effect upon the initial orientation of the pigeons. A detailed analysis of the track of each bird shows no consistent differences between birds given a clock shift and birds taken directly from the loft (table 1). In no case did any bird ever fly to its false

[1] Also, WALCOTT, C.; AND MICHENER, M. C.: Sun Navigation in Homing Pigeons—Attempts to Shift Sun Coordinates. J. Exp. Biol., vol. 54, 1971, pp. 291–316.

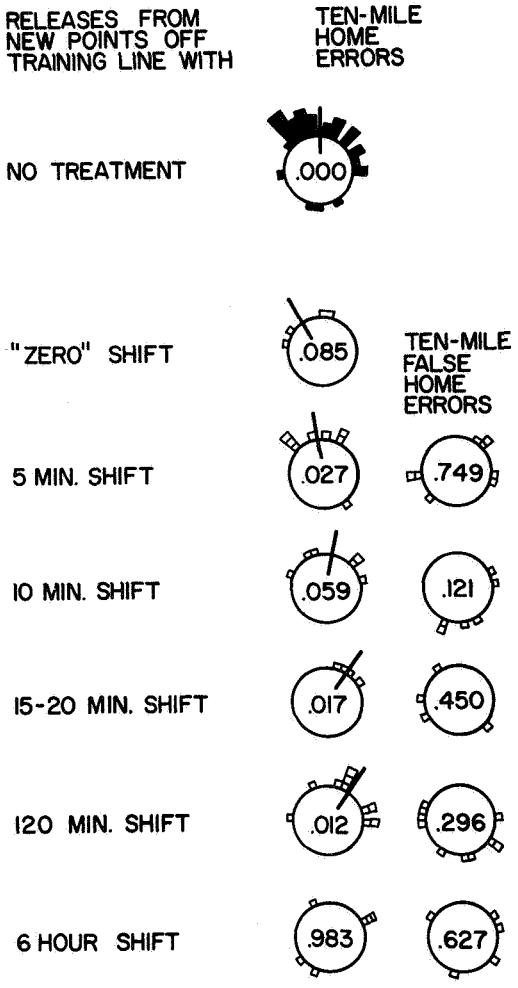

FIGURE 3. Orientation of pigeons at 10 mi from the release point after being subjected to various artificial light regimes. Left column shows bearing of each bird plotted relative to true direction to the loft; home is at the top of circle. Number in the center is probability that distribution is random: the line indicates mean bearing of distribution, given only if probability of randomness was less than 0.1. In the right-hand column, the same bearings are replotted in relation to the "false home." If birds were flying to this false home, their bearings should be tightly grouped around the top of the circle. All except the 6-hr shifted birds show better orientation to home loft than to false home.

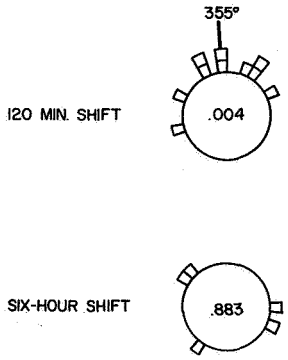

FIGURE 4. Bearings, relative to home, of birds given 2- and 6-hr shifts corrected for change in Sun azimuth caused by the shift. This procedure corrects for error the shift would have caused in a Sun compass. In the case of birds given a 120-min shift, this correction has resulted in a tighter grouping of 10-mi bearings (p is 0.004 compared with 0.012 before the correction) and a smaller difference between mean vector of distribution and the home direction (5° instead of 37°). Distribution of 6-hr shift bearings is unchanged.

home. The only consistent effect resulted from the 6-hr shifts; only two of the five birds ever homed after this treatment, and the other two homed significantly more slowly than normal. These results are in contrast with those we reported earlier (ref. 8). Apparently the small sample we reported on at that time was not typical of what we have now found. Short clock shifts had little or no effect on the birds' navigation, but larger shifts did affect the Sun compass. But Hoffmann (ref. 18) has suggested that the pigeon might use a two-clock system—one clock rigidly fixed to loft time and highly resistant to shifting which would be used for navigation, and another clock that was easily reset to local time at the release point which was to be used for a Sun-compass clock. As Snyder (ref. 19) has pointed out, it is very hard to imagine how a bird could have a clock that would be able to compensate for the constantly changing solar

TABLE 1.—*Some Aspects of the Tracks and the Homing Performance of Pigeons Subjected to Various Experimental Regimes*[a]

Treatment	Number of tracks	Homing speed	Length ratio	Tract deviation	Home/ compass ratio
No treatment	35	12.6± 9.5	1.785±1.14	21.0±18.8	23:9
Cloth box	7	11.5±10.5	1.809±1.13	15.7± 6.0	5:2
0 shift	5	6.0± 6.9	1.420±0.237	19.8± 9.9	3:1 1?
5-min shift	8	10.3±10.6	1.860±0.638	21.6±11.6	7:1
10-min shift	6	15.8±11.3	1.790±0.933	21.9±14.4	2:4
15 to 20-min shift	4	16.1± 8.8	1.756±0.577	7.0± 1.8	3:0 1?
120-min shift	10	12.3± 6.3	1.506±0.550	11.4± 9.8	7:2 1?
6-hr shift [b]	5				
Mirror box	10	5.5± 6.6	1.454±0.280	11.9± 3.5	8:2

[a] The homing speed is given in statute miles per hour followed by the standard deviation of the mean. The length ratio is the actual length of the track divided by the straight line distance from release to home. The track deviation is determined by measuring the deviation of the track from a straight line at 10 points, averaging these measurements and expressing this average as a percentage of the straight line distance from release to loft. The home/compass ratio is the number of birds whose 16-km (10-mi) bearings are closer to the home direction or closer to the trained compass direction. The three cases where these two errors are equal are indicated by ?.

[b] Only two of five birds returned.

day and still be rigidly fixed to solar time at the home loft. Indeed there is really no direct evidence to suggest that such a clock exists. But postulating the existence of such a clock, it becomes interesting to think about ways of upsetting it.

It has been shown that heavy water (D_2O) slows down the expression of the clock in a variety of organisms (refs. 20 and 21). Snyder (ref. 19) has shown that 30 percent D_2O in drinking water slows down the circadian activity rhythms of pigeons by about 4 to 6 percent. This finding led us to perform a "disruption" experiment. Pigeons were confined to a shift box with a random light schedule of the same kind used by Matthews (ref. 22). In addition, for their 10 days to 2 weeks of confinement, they were given 30 percent D_2O in their drinking water. Such birds, we reasoned, should have little recollection of time at the home loft; and not only would their clocks be running slow, but the random lights should have upset their circadian rhythms. But clearly the compass clock would also be upset by this procedure; and looking at the pigeons homing performance, it would be hard to distinguish any effect on navigation from the errors in the compass. To resolve this ambiguity, we took the pigeons from their shifting container and transported them in closed containers 400 km (250 mi) to the west where they were held for us in open cages by William Keeton at Cornell University in Ithaca, N. Y. In the week to 10 days they were held with a view of the Sun, the birds had an ample opportunity to reset their compass clocks to local Ithaca time. If their navigation clocks were also reset, they would have to be set to Ithaca time as well. At the end of 10 days the birds were equipped with transmitters and tracked from the ground and by airplane from Orange, Massachusetts, (about 88 km west of the loft and exactly on the same line as the loft) and Ithaca. Figure 5 shows the results of this release; both the experimental birds and the controls were well oriented toward the home loft. This result suggests that nei-

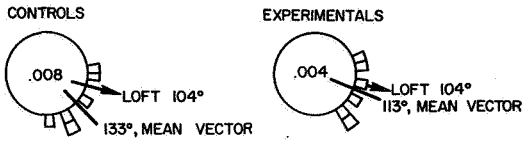

FIGURE 5. Comparison of orientation of pigeons that had been given heavy water, random light schedules, exposure to the Sun 250 miles west of the loft, and then released with pigeons taken directly from the loft. In each case the loft was at a bearing of 104° from the release site. The probability that the observed distribution arose by chance is indicated in the center of each circle: bar indicates mean vector of the pigeon's bearing at 10 mi from release. Experimental birds are as well or better oriented to the loft than the controls.

ther the D_2O, the random light schedule, nor the holding at Ithaca had any major effect on the pigeons' ability to fly home.

These experiments—the clock shifts, the disruption, and several others reported [2] (ref. 19)—suggest that the pigeons are probably not using the Sun as a navigational reference although they do seem to use it as a compass. Matthew's crucial experiments have not been successfully repeated, and indeed Keeton's (ref. 23) demonstration that shifted birds homed under total overcast strongly supports the idea that the Sun is not essential for homing. In short, considering the evidence that is currently available, it is hard to accept the view that pigeons use the Sun for navigation. This conclusion raises real questions about what the pigeons do use and where and when they obtain the information that leads them home. It might be that they are gathering information on the journey out to the release site. This seems unlikely to us because pigeons that have been carried in the back of the airplane all day while following birds released earlier homed as well as control pigeons. To examine the question further, we have transported pigeons to the release point while:

(1) Unable to see the outside
(2) Jiggled in the back of a car
(3) In varying magnetic fields
(4) While anesthetized

Such pigeons showed as accurate a homeward orientation at 8 to 16 km (5 to 10 mi) from the release site as did control pigeons taken directly from the loft. While it is obviously hard to argue that the pigeons could not have gathered any information while being transported to the release site in this way, the treatment certainly makes it less probable.

Most recently we have begun a series of experiments based on Keeton's findings (reported elsewhere in this volume) that small magnets attached to a pigeon's back sometimes cause both poor initial orientation to the loft and slower homing speeds. But the use of magnets in this way results in a rather non-uniform magnetic field around the pigeon's head. It seemed possible that a uniform field around the head might give clearer results. To produce such a uniform field, a small pair of Helmoltz coils were arranged around the pigeon's head and neck (see fig. 6), and an additional battery was added to the transmitter pack glued on the pigeon's back. A current of between 10 and 15 mA through the coils gave a field of 0.8 to 1.2 G in the region between the coils. The uniformity and magnitude of the field was measured with the small probe of a Bell gausmeter. Control birds carried coils, batteries, and connecting wires, but no current was passed through the coils. Thus the only difference between the experimentals and the controls was the presence or absence of current through the coils.

In performing the eight releases we have made to date, pigeons were taken from the

[2] WALCOTT, C.; AND MICHENER, M. C.: Sun Navigation in Homing Pigeons—Attempts to Shift Sun Coordinates. J. Exp. Biol., *ibid.*

FIGURE 6. Pigeon equipped with pair of Helmholtz coils and small radio beacon for tracking.

loft and transported to a new release site. Before each bird was released, it was equipped with coils, battery, and transmitter and then released and tracked from the ground. Experimentals and controls were released alternately, and as far as possible a bird that served as an experimental one day was used as a control the next and vice versa. This procedure enabled us to compare the performance of the same birds under both experimental and control conditions but from different release sites. The results of these preliminary experiments are shown in figures 7 and 8. An examination of the degree to which each distribution of 16-km (10-mi) vanishing points might be due to chance shows that, in seven out of the eight releases, the control birds were more closely grouped than the experimentals. Combining the results of all eight experiments in a single distrubution makes the difference in the homeward orientation of controls and experimentals clearer. In fact comparing the home errors (i.e., the number of degrees each bird's track deviates from the homeward direction) of both groups using the Mann-Whitney U test, corrected for ties, shows that the controls

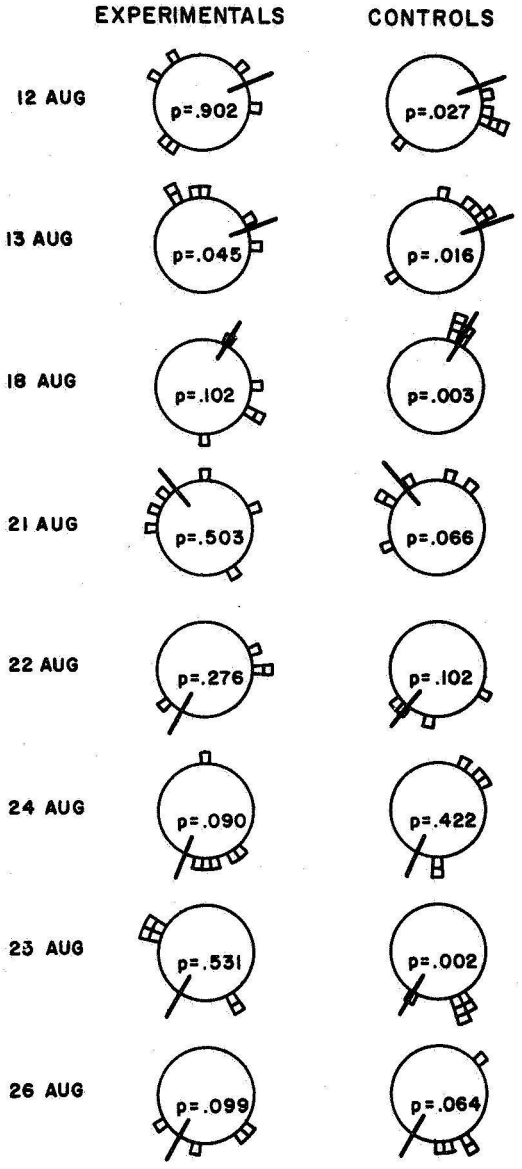

FIGURE 7. Departure bearings measured 10-mi from release points for pigeons equipped with Helmholtz coils. Both experimental and control birds were equipped with identical apparatus, but only the experimental birds had coils that were connected to batteries and were therefore carrying current. Figure in the center of each distribution is probability that observed distribution is due to chance; line indicates direction to loft.

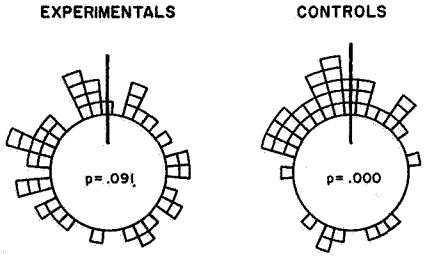

FIGURE 8. Bearings of pigeons shown in figure 7 replotted with home direction at top of diagram.

had significantly smaller home errors than the experimentals.

In addition to this difference, a number of the pigeons perched in trees when they were released. Of the 43 control birds, two sat, whereas of the 43 experimentals, 14 sat, a difference that is highly significant. The homing performance of the two groups was not significantly different. Although there is not accurate quantitative data available, it appears that all except one of the experimental birds returned with either broken coils or dead batteries whereas the majority of the control birds returned with their coils intact. These results, although based on a small number of releases, do offer the hint that magnetic fields may have some effect upon the pigeon's orientation.

To summarize our experiments to date, it seems increasingly likely that pigeons do not use the Sun as a basis of their navigation although they can make use of the Sun as a compass. Furthermore, whatever the basis of their navigation may be, information gained on the trip to the release point seems to be of less importance than cues gained at the release point itself. What the nature of these cues may be is completely unclear.

ACKNOWLEDGMENT

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DISCUSSION

GWINNER: Do you measure any circadian function to ascertain whether the pigeons' circadian rhythm(s) had in fact been shifted?

WALCOTT: Yes, we have activity rhythms which show that at least the activity rhythms were shifted about; but whether this means that the clocks were shifted or not, I don't know.

ENRIGHT: In your clock shift experiments, how long did you expose the animals to the new light cycle?

WALCOTT: About 10 days. Snyder has exposed them for a month and a half and got exactly the same shift and effects as when they were exposed for 5 days.

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Some Aspects of the Use of Visual Cues in Directional Training of Homing Pigeons[1]

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Duke University

HYPOTHESES about how birds are able to find their way home from an unfamiliar location often require the bird to make rather precise determinations of the position and/or motion of celestial bodies—usually the Sun in the case of homing piegons. Specifically Matthews (ref. 1) suggested that a pigeon could use his hypothesized system of navigation if it could detect 0.7° difference in altitude and 1.2° difference in azimuth of the Sun. Pennycuick ref. 2) suggested 12′ of altitude and 1.5″ of arc per minute as minimum differences the bird would need to detect to use his proposed system of navigation to as little as 12 n. mi. from home. Meyer (ref. 3) reported that homing pigeons were able to discriminate a difference in altitude of a projected light of 30″, and a difference in arc angle of 1°.

This paper reports an investigation aimed at determining how accurately homing pigeons (*Columba livia*) can in fact measure the position of a light source, and what cues are used in making the measurements.

[1] This paper was presented by Klaus Schmidt-Koenig.

EXPERIMENT 1

The subjects were homing pigeons chosen from the Duke University and Wilhelmshaven stocks kept at Duke University. All pigeons except numbers 6 and 11 made successful homing flights of up to 200 km, either before or after these experiments. The birds had not previously been used in any other training work.

The technique used is similar to a method used to obtain psychophysical thresholds from a variety of animals (refs. 4 to 6). Details of the technique have been described elsewhere (ref. 7).[2] Briefly, the pigeon sat on a circular table in a small box with its head through a slit in the front of the box (fig. 1). On top of the table in front of the pigeon were two pecking keys (A and B) and a food reward cup. The pigeon was conditioned to peck key A if the position of the light source (relative to the bird's own orientation) was in a se-

[2] McDONALD, D. L.: Some Aspects of the Use of Visual Cues in Directional Training of Homing Pigeons. Unpublished Ph.D. dissertation, Duke University, 1970.

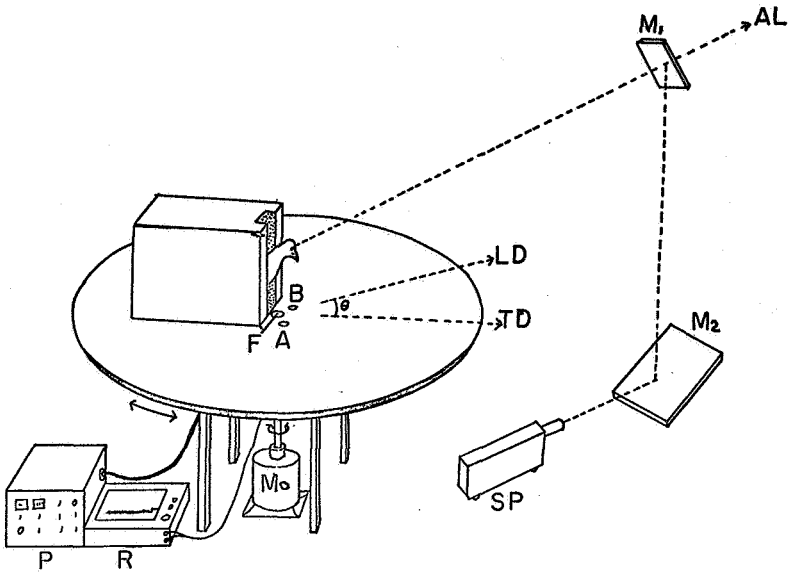

FIGURE 1. Diagrammatic representation of experimental arrangement: A and B, response keys; F, food-reward cup; LD, direction of the light; TD, trained direction; θ, angle between trained and light directions; SP, slide projector; M_1 and M_2, mirrors; AL, apparent light; P, programmer; R, position recorder; Mo, motor.

lected position called the trained position, and to peck key B if the light was not in the trained position. Pecks on key A moved the light source away from the trained position; pecks on key B, toward the trained position. Thus if the bird detected that the relative position of the light source was not in the trained position, it pecked key B, moving the light source closer to the trained position by small steps, one step for each peck. Eventually the bird was not able to discriminate the position of the light source from the trained position, and began to peck key A, moving the light source away from the trained position by small steps. This continued back and forth, oscillating about the average position which the bird could not discriminate from the trained position. The behavior was reinforced by food rewards. Four to 10 pecks were required on each key for the bird to get a food reward.

Training was quite slow. The birds were worked for about ½ hr each day. About 2 weeks of training was required until the birds showed signs of learning the discrimination. The entire experiment took 35 to 45 days from start of training until the data had been collected.

The light source used was a slide projector utilizing a 500-W lamp. The slide projector sat on top of a large truncated cone made from a metal frame covered by white cloth (fig. 2). The light was projected onto the bird through a series of seven mirrors. By moving its head through a maximum of 7.5 cm to each side, the pigeon observed a parallax movement of only 1°.

During nearly every training session, a diagnostic test was performed to check on whether the pigeon was in fact using the relative position of the light source as the cue for the discrimination. The test was per-

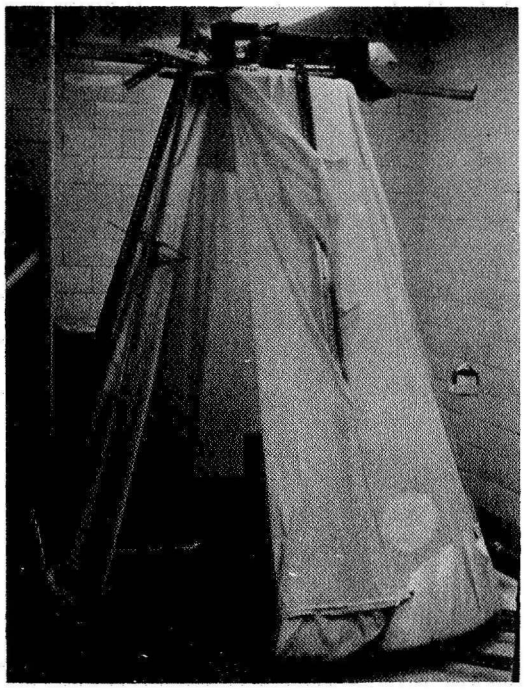

FIGURE 2. Slide projector used as light source is mounted on top of framework. Rotating table and pigeon's box can be seen through folded-back sheet which zipped closed when the birds were working. Small arrow points to last mirror in the series, which could be moved up and down the track on which it is mounted to change the altitude of the light.

formed by moving the light source far away from the position at which the pigeon had set it. The bird was correctly performing the discrimination if it immediately reset the light source to its pretest relative position (fig. 3).

A continuous record of the orientation of the table was made by plotting on a recording (VOM) the resistance of a precision potentiometer coupled to the rotation of the table. The orientation of the table could be read to 0.1° of the true orientation.

In order to calculate an average direction about which the pigeon oscillated, a frequency distribution of the number of times the table was pointed in different directions was constructed. This was done by counting the number of times the recorded trace crossed each of the lengthwise lines on the chart paper. These lines were approximately 0.286° apart, giving 0.286° per class interval.

Results

The pigeons were trained to adjust the relative position of the light source to three different positions.

(1) The trained position of the light source for pigeons 6 and 11 was 62° relative azimuth counterclockwise from the longitudinal axis of the box in which the pigeon sat. The relative azimuth of the light source was changed by rotating the table on which the bird was placed. Pecks on key A rotated the table counterclockwise; on key B, clockwise. (The altitude of the light source was held at a constant 21°.) Pigeon 6 could discriminate the relative azimuth of the light source from the trained position when they differed by only 3.4°, on the average. Pigeon 11's performance was similar, discriminating a difference of 3.6°.

(2) The trained position of the light for pigeons 121 and 122 was 19° altitude above horizontal. Pecks on key A moved the altitude higher than 19°; on key B, closer to 19°. (The light remained a constant 40° clockwise for these birds.) Pigeon 121 could discriminate the altitude of the light from the trained altitude when they differed by as little as 8°; Pigeon 122, when they differed by as little as 11°.

(3) The trained position for pigeon 51 was 40° relative azimuth clockwise and an altitude of 21°. Pecks on key A rotated the light clockwise around the bird (by rotating the entire cone) and raised the altitude; pecks on B rotated the light counterclockwise and lowered the altitude. The movements

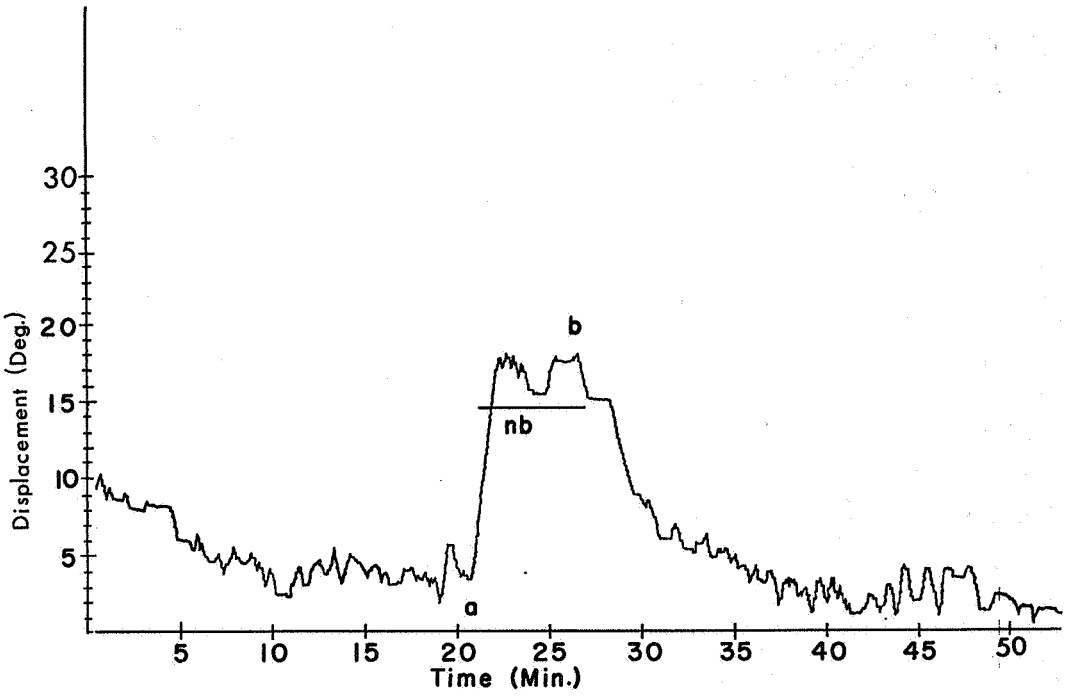

FIGURE 3. Example of correct response in a diagnostic test. At point a, light source was rotated 14.5° counerclockwise around the pigeon; nb, the new baseline. Bird quickly resets relative position between itself and light source to what it was before light was moved. At b, light was returned to original position, and bird again adjusts correctly.

were directly coupled. Pigeon 51 adjusted the light on the average to 5.1° difference from the trained relative azimuth and 9.0° from the trained altitude. Investigation showed that only the altitude of the light source was being used for the discrimination. If the relative azimuth were held constant, the bird would adjust the altitude in a normal manner; but if the altitude was held constant and the relative azimuth alone allowed to vary, the bird became confused.

The results are tabulated in table 1.

Discussion

The data collected here do not compare favorably with the limits of 0.7° difference in altitude and 1.2° difference in azimuth that Matthews (ref. 1) suggested a pigeon would need to detect. Neither do they compare well with the 12′ difference in altitude suggested by Pennycuick (ref. 2). The results are also not as good as those reported by Meyer (ref. 3), where pigeons could discriminate a difference of 30′ altitude and 1° azimuth. As will be shown next, the use of shadows was important in the discriminations reported here. It is doubtful if shadows were important in Meyer's study, since the light was projected onto a screen rather than onto the bird itself. Thus the birds could well have been responding to different stimuli in the two studies.

Observations on Pigeon 6

Careful observations were made of pigeon 6 while it was working in the apparatus. The observations were made through a small peep-

hole without disturbing the pigeon. This pigeon always drew its head inside the box and pecked on the inside wall between pecks on the response keys. These movements resembled superstitious behavior; i.e., irrelevant behavior patterns that are maintained by inadvertent reinforcement. However, closer observations suggested that the pigeon was directing the pecks at a small lighted area on the inside wall of the box, which was illuminated by light passing through the slot in the front of the box (fig. 4). This lighted area moved along the wall in correlation with the rotation of the table, and thus was a potential source of cues that could be used for the discrimination. To test this idea, a panelescent light was installed on the inside wall of the box. This light is a thin panel that emits a soft green light when connected to a power source. When the panelescent light was turned on, the contrast between the above described lighted area and the rest of the wall was obliterated. The pigeon was kept in the box with the light on for several hours so it would become accustomed to its presence. Also the bird was worked for five sessions with the panel in place but its light off to make certain that the presence of the panel did not affect its performance. Figure 5 shows the results of one test when the panelescent light was turned on during the normal working session of the bird. Three such tests were done, each with the same results; i.e., the pigeon pecked key A continuously

TABLE 1.—*Average Performances of Pigeons in Experiment 1*

Pigeon number	n[a]	Azimuth (degrees)		Altitude (degrees)	
		x		x[b]	Sx[c]
6	7	3.4	0.5	.....	
11	31	3.6	1.5	.....	
51	14	5.1	1.8	9.0	.....
121	10	.....		8.0	2.9
122	7	.....		11.0	2.8

[a] Number of trials, where each trial is the average performance during a day's session of ½ to 1 hr

[b] Average difference between the actual position and the trained position of the light source that the pigeon could discriminate. The average performance for a single day was used as one datum in calculating x

[c] Standard deviation of the n trials

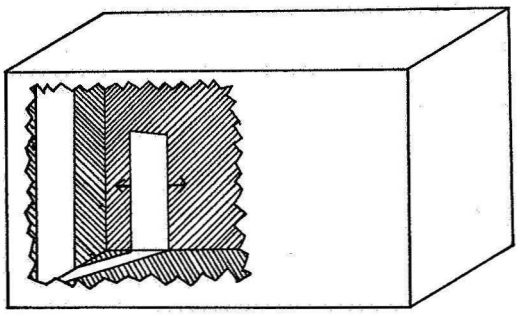

FIGURE 4. Cutaway drawing of the training box, showing lighted area to which pigeon 6 was attending. As the box rotated, lighted area moved along inside wall of the box in direction of arrows; width of lighted area varied with rotation.

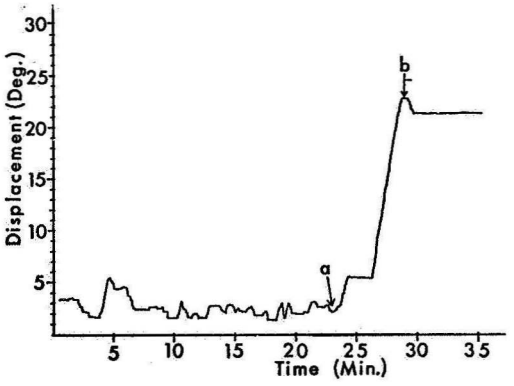

FIGURE 5. Result of turning the panelescent on for pigeon 6. At point a light was turned on; at point b, off.

after the panelescent light was turned on. The behavior of pulling the head inside the box and pecking on the wall also disappeared.

Three other tests were done in which a panelescent light on the opposite wall from the lighted area was turned on. This had the effect of dimming the contrast between the lighted and unlighted areas, but not obliterating them completely. The response was similar to the previous tests in that the bird pecked only key A. However, the pecking behavior on the inside wall continued, although the pecks were directed at the inside front corner of the box.

This evidence indicated that the stimulus to which the pigeon was attending was the position of the lighted area on the wall of the box. Thus the pigeon would observe that when it pecked key A, the area would move toward the back of the box; key B, toward the front. When the panelescent lights were turned on, it appeared as if the area had moved to the extreme forward edge of the wall, even beyond the trained position. This would lead to the continuous pecks on key A.

Observations on Pigeon 11

Pigeon 11 rarely pulled its head inside the box as did pigeon 6. However, the bird frequently appeared to look at the outside right front corner of the box. This led me to suspect that the pattern of the shadows on the top of the table might be supplying cues to the bird. The normal configuration of the lighted area had a long bar of light that projected past the box. This bar of light varied in width and angle to the box as the table rotated, and seemed a likely candidate for a source of cues (fig. 6A). A 6-W electric lamp was mounted on the outside of the box in such a way to obscure this lighted area (fig. 6B). When this lamp was turned on, the bird

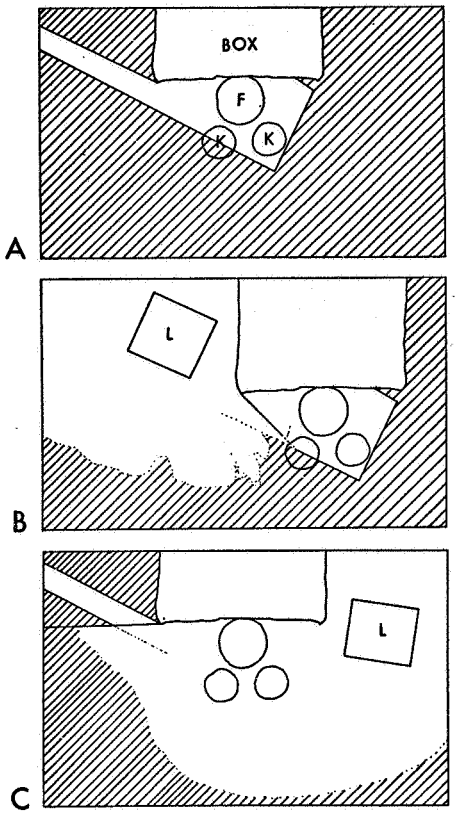

FIGURE 6. Shadow patterns for pigeon 11 (looking down on top of box and table). (A) Normal pattern at training direction. (B) Pattern with light on right side of box. (C) Pattern with light on left side of box. K, pecking key; F, food cup; L, 6-W electric lamp.

responded by pecking on key A, which seemed to confirm the importance of this cue. However, when the light was mounted on the left side of the box so as to obscure all of the lighted area except the bar projecting past the box (fig. 6C), the pigeon still pecked key A continuously.

Taking a different approach, the configuration of the lighted area was changed as in figure 7B. This increased the width of the bar of light from 15 mm to 35 mm. The bird responded by pecking key A until it was

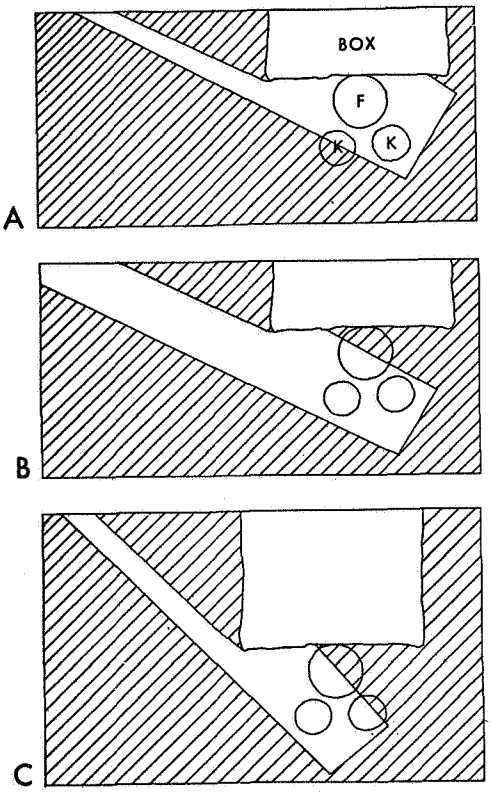

FIGURE 7. Effect of changing shape of lighted area for pigeon 11. (A) Normal shape of lighted area at training direction. (B) Experimental shape of lighted area at training direction. (C) Shape of lighted area after stabilization under experimental conditions.

about 19° from the training direction. At his position, the pattern of shadows was as shown in figure 7C. The width of the bar of light was about 16 mm, close to the width at the trained direction under normal condition. However, the angle between the box and the bar of light was 19° less than normal.

Inspection of figure 6 reveals that there is a small part of the lighted area directly in front of the right front corner of the box that was obscured when the 6-W light was on both the right and left side. This is the same location at which the bird seemed to look between pecks. The width of the lighted area at this location may well be the cue to which the bird was responding. If the area was too narrow, the bird pecked key B, rotating the table clockwise and making the bar wider. If the bird could not discriminate the width of the area from the width when at the trained direction, it would peck key A. In figures 7B and C, the lighted area was much wider than normal, seemingly indicating that the table was well beyond the trained direction. This would lead to continuous pecks on key A, which was observed.

Observations on Pigeon 121

Pigeon 121 pecked at the cover over key A between responses. It was noted that a shadow was cast on this cover by the edge of the hole in the table through which the key was pecked. As the altitude of the light changed, the edge of the shadow moved across the cover. When the altitude was 10° above the trained altitude of 19°, the edge of the shadow was 4 mm from the edge of the hole opposite the light.

A piece of black paper 9 mm high was placed on the edge of the hole nearest the light so that the entire cover over key A was in shadow. The pigeon responded by positioning the light to 50° altitude (fig. 8). The edge of the shadow, now cast by the top edge of the black paper, was found to be slightly greater than 4 mm from the edge of the hole. Thus the pigeon seemed to be attending to the position of the shadow on the cover over key A, and not directly to the altitude of the light source.

EXPERIMENT 2

Evidence was presented above that pigeons 6, 11, and 121 attended to the shadow patterns in making their discriminations. This

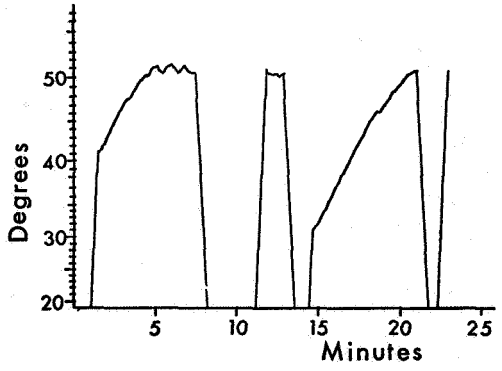

FIGURE 8. Response of pigeon 121 to changes in shadow pattern. Under normal conditions, pigeon oscillated about 27°. Each time recording line fell to 19°, pigeon was given a food reward to maintain responding.

TABLE 2.—*Response of Pigeons When All Shadows Were Eliminated and the Relative Position of the Light Source Was Changed*

Test	Response when lights on				Response when lights turned off			
	Pigeon number				Pigeon number			
	11	51	121	122	11	51	121	122
1	C	C	B	B	A [a]	A	A [a]	A [a]
2	C [b]	B	C	C	A [a]	A	A	A
3	B	B	D	C	A	A	A	B
4	C	C	B	C	A	A	A	A [a]
5	B	C	D	C	A	A	A	A

Notes:

A—Returned light to normal position. In the case of pigeon 11, the table was rotated rather than the light being moved.

B—Did not return light to normal position but continued to peck keys, keeping the light in about the same position

C—Pecked continuously on key A or B, driving the light far beyond normal position

D—Did nothing

[a] The pigeon had started to return the light but was interrupted by termination of the experiment

[b] Results of this test were ambiguous.

experiment was performed to verify that shadows were indeed important for these birds (except pigeon 6, which was not available for the experiment), and to investigate whether shadows were also being used by pigeons 51 and 122.

Apparatus

The apparatus was set up as in Experiment 1. In addition, two 15-W flourescent lights were placed under the table. When these lights were turned on, the inside of the cone was indirectly lighted, and the shadows on the table top were obscured so that they were invisible to the human eye.

Procedure

The experiment lasted 10 days. On the first day, and alternate days thereafter, the birds were worked as usual, with diagnostic tests being done to verify they were under control of the light stimulus. On the second day, and alternate days thereafter, the indirect lighting was turned on at the same time as the relative position of the light source was changed for the diagnostic test. After the nature of the bird's response became clear, the indirect lighting was turned off again, and the bird's response noted.

Results

The results are presented in table 2. In every case, the pigeons did something other than return the light to its normal relative position when the indirect lighting was on. Usually the pigeons continued pecking after the flourescent lights were turned on, indicating that they were not unduly startled by turning the lights on. Two exceptions are tests 3 and 5 for pigeon 121, where the response of doing nothing could be interpeted

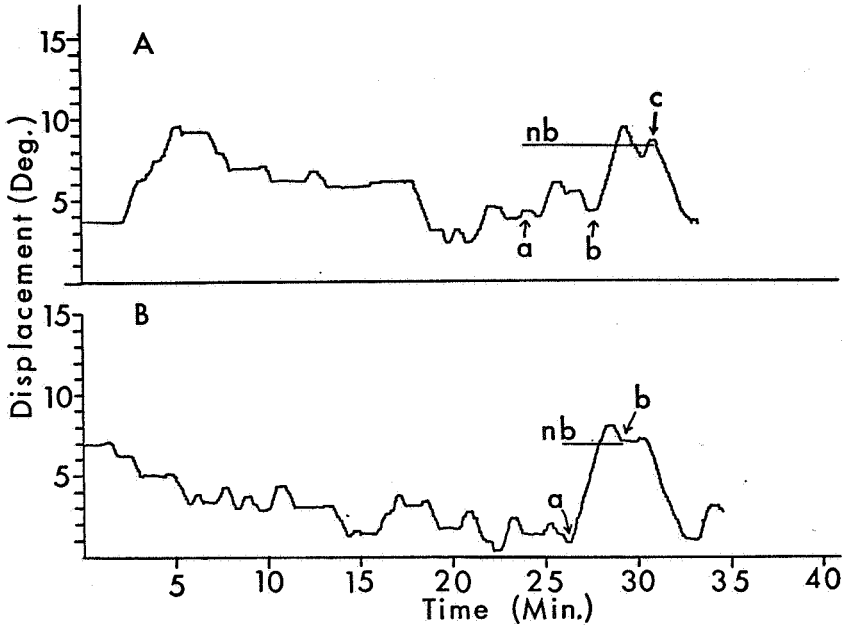

FIGURE 9. Typical response of pigeon 11 in experiment 2. A: At point a, indirect lighting was turned on, and the stimulus light moved 8° counterclockwise to new baseline (nb). At point b, indirect lighting was turned off, and the pigeon reset the table to near normal position. At point c, stimulus light was returned to original position, and pigeon appropriately reset the table. B: At point a, stimulus light was moved 7° counterclockwise, but indirect lighting was not turned on. The bird immediately responds to reset the table. At point b, table was returned to original position.

as a startle response. Distress calls were also noted in these two cases.

The reaction of the pigeons when the indirect lighting was turned off was dramatic. In all but one case, they returned the light to the normal position. Often this response began immediately after the indirect lighting was turned off, and the bird pecked the correct key rapidly and without interruption until the light was in the normal position (fig. 9).

EXPERIMENT 3

The purpose of this experiment was to see how well pigeons could measure the angle between their position and the direction of a light source in a shadowless environment. The task was identical to that for pigeons 6 and 11 in Experiment 1 so comparisons could be made.

Subjects

Three homing pigeons from the Duke University stock of pigeons, numbers 89, 94, and 95, were used. All birds were experimentally naive and had never made a homing flight.

Apparatus

The apparatus was that used in Experiment 1, except the indirect lighting used in

Experiment 2 was on at all times. In addition, two layers of cheesecloth surrounded the table upon which the bird sat in order to obscure details on the inside of the surrounding cloth that might be used as cues by the bird. The light from the slide projector could be readily seen through the cheesecloth.

Procedure and Results

The training procedure was like that used in Experiment 1. The three pigeons quickly learned to peck keys A and B for food rewards, but when changing of the pecking behavior for A and B was attempted, learning became very slow. After a total of 9½ hr of training, the birds had each learned to peck key B twice and be rotated to the training direction, then peck key A twice for a food reward. However, when the number of pecks required on each key was increased, the pigeons became confused and their responses rapidly extinguished. This suggested that they had merely learned that two pecks on key B followed by two on key A would yield a food reward. Also, when the stimulus light was rotated around the birds in a diagnostic test, the pigeons did not reposition the table to maintain the trained relative azimuth. Even when the stimulus light was turned off, the pigeons continued to peck in the same manner as when it was on. How much more training would have been required to learn the task is not known. It is possible that the addition of the cheesecloth between the bird and the stimulus light is responsible for the slower learning.

For purposes of comparison, an average of 7 hr of training was required for pigeons 11, 51, 121, and 122 to successfully learn to peck twice on each key to get a food reward. More important, diagnostic tests indicated that these birds were correctly responding to the relative azimuth of the stimulus light (or as shown in Experiment 2, the shadow patterns).

CONCLUSION

The experiments above provide conclusive evidence that all of the birds trained indoors were attending to shadows and suggests that the use of shadows may be a basic mechanism by which homing pigeons derive cues from a light source such as the Sun. This is supported by the evidence in Experiment 3, which suggests that learning to orient in a shadowless environment may, at the least, be more difficult than when shadows are present. In addition, these experiments raise the question of whether the many other experiments done in orientation cages also involved the use of shadows as cues. Training work done by Kramer (ref. 8) with starlings, Kramer and Riese (ref. 9) with pigeons, von St. Paul (ref. 10) with Western Meadowlarks, and Hoffmann (ref. 11) with starlings all involved the use of the same type of orientation cage. This cage had 12 feeders arranged around the periphery of the apparatus and a wire frame to hold up the netting. In all of these cases, whether used indoors or under natural skies, distinct shadows that could have been used by the birds for orientational cues were undoubtedly available. Even the bird's own shadow could give the same kind of directional cues. The apparatus that Matthews (ref. 12) used for indoor directional training (relative azimuth to a 60-W light bulb) would have had many shadows. Hamilton (ref. 13) reports that directionally trained ducklings were disoriented when they could not see the Sun directly but still could see the shadows on the walls of the apparatus. Also it appeared that the ducklings intentionally walked into the sunlight before making a directional choice.[3]

[3] Personal communication with W. J. Hamilton.

However, the shadow patterns on the floor or those cast by the duckling itself would also disappear when the Sun was too low, and the possibility cannot be excluded that these were used for orientation. The directional training experiments done by Schmidt-Koenig (refs. 14 to 16) using a different technique also allowed the possibility of shadows giving directional cues.

On the basis of the evidence presented here, it is impossible to say whether the use of shadows for the directional discriminations has any relevance to the mechanisms used by pigeons in homing flights. It might well be argued that when birds are directionally trained, they simply perform the task that has been taught to them. If shadows are available, the birds may learn to respond to them even if shadows play no role in homing orientation or navigation.

Most of the evidence in orientation work that implicates the position or motion of the Sun as important for orientation would apply equally well to shadows. Seldom is the Sun visible without casting shadows. The compensation for the daily movement of the Sun could well be compensation for the movement of shadows. The kinds of orientation schemes proposed by Matthews (ref. 1) or Pennycuick (ref. 2) could apply equally well to the use of shadows. The hypotheses would then suggest that the pigeons learn the length and orientation of shadows at the release site, and fly in a direction that would return the observed shadows to the same conditions as remembered for home. The shadows could be those cast by trees or buildings or even the shadow cast by the bird itself. (The bird would need to adjust for the height of objects casting the shadows.) If the bird were measuring the changes in the altitude of the Sun, using the length of the shadows would exaggerate the movement. For example, let us assume the bird wishes to measure the movement of the Sun at 8:00 a.m. at equinox at 36° N latitude. At 8:00 a.m. the altitude is 23° 52'. Four minutes later the altitude is 24° 38'. Thus the altitude of the Sun changes through a visual angle of 46'. Now let us further assume that the bird is flying at treetop level 20 m above the ground. At 8:00 a.m., a tree 20 m tall casts a shadow 45.2 m long; and at 8:04 a.m., the same tree casts a shadow 43.6 m long. The length of the shadow decreases by 1.6 m, which subtends a visual angle of 4° 34' for the bird flying at 20 m. Thus the visual angle subtended by the movement is nearly six times larger when shadows are used instead of viewing the Sun directly.

If the use of shadows is merely an artifact of experimental conditions, it is a variable that will require rigorous control in future directional training work.

ACKNOWLEDGMENT

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DISCUSSION

NORRIS: Are there any studies that would reflect which way a pigeon looks when flying? Is it possible that they would be disoriented when prevented from looking down, for instance?

SCHMIDT-KOENIG: There are preliminary accounts of some experiments that we are in the process of doing. If you block the pigeon's view by blackening the lower half of its eye, it is still almost as good as the control.

CARR: Are there any experiments that actually have tested discrimination of the rate of change in

angles by a process of remembering a former position and comparing it with a new position?

SCHMIDT-KOENIG: Meyer's work has some relation to this.

BULLOCK: It is known that some invertebrates can detect very slow movement, slower than the Sun across the sky. Several kinds of animals have been studied and shown to do this in behavioral as well as physiological experiments including cephalopods, locusts, and crabs. There are also experiments in which the animals' memory of the position of an object is sufficient to be able to detect a small change in position that took place during a period up to minutes in the dark.

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Biology Can Use Trained Animals[1]

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Harvard University

ANIMALS (especially the higher ones) tend to do whatever earns them reward and avoid whatever leads to punishment. This commonplace observation has, for about 75 yr (ref. 1), tantalized psychologists with the promise of a useful and enlightening science. To fulfill the promise, psychology studies the nature of rewards and punishments, their interrelationships, the underlying physiological machinery, the differences and similarities among species in these respects, the relations between current behavior and past rewards and punishments, and so on. None of these subjects, however, will concern me here, for the theme of this paper is not to summarize how our science is progressing, but to show that there already exists a technology of reward and punishment that is simply waiting for application in other fields of biology, particularly when questions of sensory or motor capacity are involved. My case will rest on several examples, already in the psychological literature, in which the use of trained animals has solved problems not easily solved by more common biological procedures.

The experimental paradigm was perfected by B.F. Skinner in the early 1930's (ref. 2), working not in a psychological laboratory, but in W.J. Crozier's laboratory for general physiology. The original "Skinner box" was a chamber measuring about 0.3m' cubed into which a hungry rat was placed and simply allowed to move freely about (ref. 3). Protruding through a wall of the chamber was a horizontal lever that could be depressed and thereby operate a device that dropped a food pellet down a chute and within the rat's reach. Acting in accordance with principles that need not be explicated here, a rat in the box quickly learns to depress the lever with fair regularity, until its hunger is spent. Now imagine a slightly more complex procedure. Suppose pressing the lever is rewarded only when a lamp is turned on and off from time to time, at irregular intervals and independent of the rat's behavior. The pattern of reward and non-reward follows along. After a little practice, the rat is guided by the lamp, pressing much more in the light than in the dark. Note, however, that the relation is arbitrary. The absence of light could just as well have been made the signal for work, if reward had been correlated with darkness and non-reward with light. How reliably the rat obeys the lamp

[1] The author was assisted in the preparation of this paper by grants from NASA and NIMH to Harvard University.

depends on many factors—the degree of hunger, the amount of work involved in pressing the lever, the rate and pattern of lamp on and off, the size and composition of the food pellet, the schedule of reward, and, no doubt, factors not yet identified. However, the lamp's power to control responding also depends upon the rat's visual sensitivity and the size of the stimulus change. If the light is very dim, then turning it on and off will control behavior less decisively than if the light is quite bright, all other factors held constant. In the limiting case, if the light is dimmer than the minimum visible intensity, then lever pressing will simply occur independently of the state of the lamp, for the rat can hardly attend to a light it cannot see.

This hypothetical experiment is supposed to suggest how a training procedure may be applied to a question of sensory process, in this instance a visual threshold. The remainder of the paper deals with actual experiments, in which the procedures are usually (but not always) a good deal more complicated. Among other things, I hope to show that the complexity is appropriate to the task, which is to say that the experiments use the simplest procedure for getting at the desired question.

SENSORY CAPACITY

The first experiment I would like to describe was done by a Harvard undergraduate (ref. 4) who wanted to know whether pigeons can smell, a question that had not yet been unequivocally answered. Since some of the mystery surrounding animal navigation and orientation is similarly a question of sensory capacity, Michelsen's work has special relevance here. Olfaction in birds, in spite of the interest and scientific efforts of such eminent figures as Audubon in the 19th century and Grey Walter in the 20th, was still an open question when Michelsen undertook his research. The apparent ability of birds to find or flee from odorous objects, like carrion or predators, could be based on smell or on other sensory modalities—sight or hearing in particular—and the relevant evidence was ambiguous. Michelsen's approach was to devise a training procedure such that if a pigeon can smell, then it would learn a correlation between the odorant and reward, but that if it is without a sense of smell, its responding would be random.

Figure 1 shows the pigeon's eye view of the front of the experimental chamber, of which the internal geography was crucial for the success of the procedure. On one wall were three switches (1,2,3) that the pigeons were trained to peck at in a manner to be described later. The square (B) was a feeding device that could be activated for brief periods, at which times the pigeon would eat. Two of the three switches (1,2) were in a partially enclosed cylinder. The pigeon could get at these two switches only by inserting its head through an opening (A) in the cylinder. Also inside the cylinder was the access to the feeding device, but food was found there only when the procedure called for reward. The third switch (3) was beside the cylinder, available for responding while the pigeon did not have its head in the cylinder. There were also two sources of illumination: one inside the cylinder (E) and the other outside (not shown). The cylinder was constructed so that a stream of gas piped into it from the top (C) was exhausted from its bottom. In addition, several exhaust fans could evacuate any lingering gasses from the general interior of the chamber.

The testing procedure involved a sequence of responses and stimulus changes, as follows. At the beginning of a trial, the general chamber light is on, but the interior of the cylinder is dark. A peck at the switch (3)

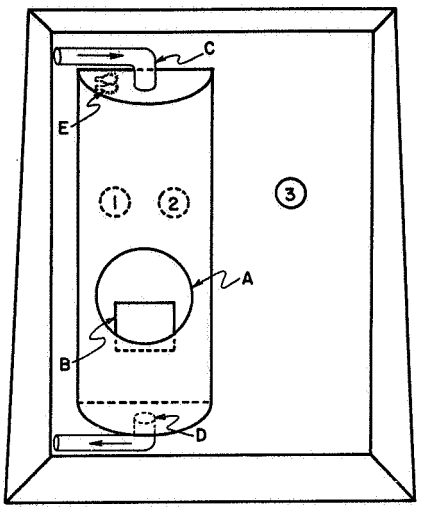

FIGURE 1. Interior view of front wall of apparatus for studying olfaction in pigeons. Redrawn from Michelsen (ref. 4).

outside the cylinder starts the flow of gas within the cylinder, and also starts a nine-second timer. At the end of the nine-second period, a peck on switch (3) turns the lights off outside the cylinder, illuminates the inside of the cylinder and thereby signals to the pigeon that the switches inside the cylinder are operative. The pigeon will then insert its head into the cylinder to peck at either of the two inside switches.[2] If the stream of gas contains an odorant, then the seventh peck at the left switch is rewarded; if it does not contain an odorant, then the seventh peck at the right switch is rewarded. However, in any case, a fourth incorrect peck before the seventh correct peck terminates the trial without any reward at all. The reason for this seemingly arbitrary asymmetry of correct and incorrect responses is that it penalizes the pigeon for alternating randomly between the two switches. If the criterion for right and wrong were equal, then the pigeon would be rewarded half the time for just random responding. With asymmetry, the likelihood of reward for random responding is quite low, apparently low enough so random responding is precluded, as Michelsen's results showed.

At the end of a trial the gas stream is shut off and there is a one-minute rest period, during which the exhaust fans cleanse the chamber of any lingering odors. On any given trial, the gas stream either contained an odorant or else air passed through distilled water. Whenever a trial ended in failure, the stimulus conditions were repeated for the next trial. After a successful trial, the next trial randomly presented the odorant or the non-odorant. The reason for this procedural complication, called a "correction procedure," is to keep the pigeon from always choosing just one switch. Without the correction procedure, a pigeon which responded to just switch (1) or just switch (2) all the time would, given the random alternation of stimulus conditions, be rewarded on half the trials. And being right half the time is good enough for most pigeons, so they would not bother to learn that by attending to the presence or absence of the odorant, they could be right up to 100 percent of the time. With the correction procedure, however, such perseverative responding would soon lead to no reward at all, for as soon as responding was on the wrong switch, then perseveration would prevent the stimulus condition from changing.

Michelsen tried several different odorants and found that performance levelled off at about 85 to 90 percent of the trials correct, with chance dictating 50 percent (discount-

[2] The intermediate stages of training will not be described here, neither for this experiment nor the others to follow. Usually, the final procedures must be approached in small increments allowing the subject to become thoroughly acclimated at each level. Unfortunately, there appears to be no general rule for this process of successive approximation. Some points can, however, be found in Skinner (ref. 5).

ing trials repeated because of the correction procedure). The more irritating odors—like sec-butyl acetate—got a somewhat better score than the milder odors—like isooctane. No doubt, trigeminal nerve irritation simply added to olfactory nerve stimulation, probably more so for irritants like sec-butyl acetate. However, the discrimination in all cases was unmistakable. Various control procedures confirmed that the stimulus was the odorant itself in the air stream, and not some procedural or apparatus artifact. Of course, such artifacts cannot be absolutely excluded, but a reasonably thorough search failed to uncover any.

The conclusion of the study is that pigeons, and therefore probably other birds, possess a sense of smell, which is reassuring, given the well-developed olfactory bulbs that many birds have. However, until this study had been done, the apparent neurological basis for olfaction was not evidence of olfaction, but only a hint of it. A sense modality is, in the last analysis, a psychological phenomenon, not a physiological organ. This is not to deny the physiological basis of sensation or any psychological process, but to note that the *sine qua non* of a sense is some sort of behavioral manifestation.

Michelsen's experiment illustrates a number of key ingredients in the use of behavioral techniques for answering questions of sensory capacity, and is therefore worthy of some further consideration. The only points of contact between the experimenter and the subject are the contingencies of stimulation and reward. The pigeon responds so as to be rewarded, but it cannot be assumed that it will attend to stimuli unless doing so has some significant effect on the outcome. In fact, all other things being equal, the animal is disposed not to attend to redundant stimulation.

How to arrange the dependency between stimulus and reward and how much difference attention is to make are important practical questions, unfortunately without general answers, only specific ones for specific questions. The skillful experimenter is guided by his subject's behavior toward the optimal level of complexity, where the subject is maximally disposed to attend to the relevant stimuli. Michelsen's procedure is the outcome of such an interaction between subject and experimenter. Thus, the asymmetry of the criteria for right and wrong trials discouraged random responding. Because it took seven pecks to be right and only four pecks to be wrong, there was a significant premium for paying attention to the olfactory stimuli as compared to just random responding. The correction procedure similarly kept the pigeon focussed on the right aspect of the situation, from the experimenter's viewpoint. Without it, responding could have become stereotyped and still be rewarded half the time. Other features of the procedure, although mainly concerning matters of housekeeping, were also important. The third switch and its associated nine-second interval held the pigeon and the presentation of the stimulus in the cylinder in phase with each other. By letting the pigeon pace the experiment, the stimuli to be attended to were only presented when the subject was ready to work.

LIMITS OF SENSORY CAPACITY

Michelsen's experiment is a good model for finding out whether an animal has a sensory capacity at all. Obviously, any adaptation of it must take into account the nature of the stimulation at question. Delivering an odor is not much like delivering a magnetic field or indicating a compass direction; but careful analysis and trial and error should extend the method to other instances. The basic notion of using the animal's interest in

being rewarded to find out about its sensory processes is, however, far from limited to such simple questions as whether a given sense exists. Because it exemplifies a more exacting field of study, I should like to describe an experiment by Blough (ref. 6) that traced the course of visual dark adaptation in pigeons. The question is not whether vision is present in general, but what is the absolute visual threshold from moment to moment.

The experimental chamber permitted the showing of visual stimuli under precise control. As in Michelsen's apparatus, there was an enclosure (see figure 2) into which the pigeon had to insert its head to get at the response switches (A,B) and the feeder, and within which the stimuli were presented. Once inside the enclosure, the pigeon could look at a stimulus patch which provided the sole source of illumination for the chamber. The function of the shutter, wedge, and record are described below.

Blough's procedure is an adaptation of Békésy's method for tracing the absolute auditory threshold, which is the standard measurement of clinical audiometry. The human subject for an audiogram wears a pair of earphones and listens for a pure tone whose intensity grows with the passage of time. He is instructed to press a button if he hears the tone, but pressing the button drives the intensity of the tone down. When the tone drops below his absolute auditory threshold, he no longer hears it and should therefore release the button, which allows the tone to resume its upward course. The interaction of subject and apparatus thus produces a tone whose intensity fluctuates around the absolute threshold. In standard audiometry, the frequency of the tone sweeps up and down the audible range, so as to give the clinical audiogram, but other parameters, of the stimulus or the subject himself, may be varied instead.

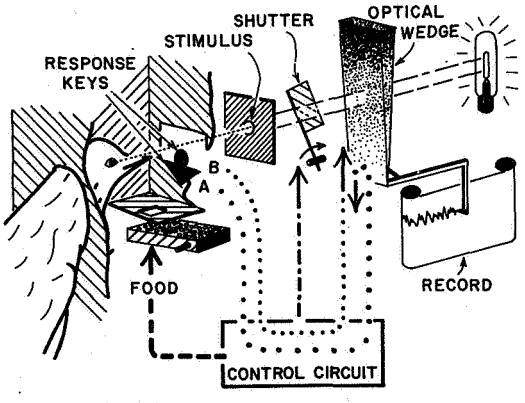

FIGURE 2. Schematic rendering of apparatus for tracing visual dark adaptation in pigeons. Redrawn from Blough (ref. 6).

Blough's problem was to find a way to instruct the pigeon to keep the light similarly at the threshold, but his only points of contact were the contingencies of stimulation and reward. The pecking of one switch (key A) reduced the intensity of the light by driving the optical wedge (usually by a small amount like 0.03 log units), while the pecking of the other (key B) increased it (by an equal amount.) This differs from Békésy's method, in which the stimulus intensity rose simply with the passage of time, by having both decrements and increments produced by discrete response. If the pigeon ceased pecking, the light would hold at its current intensity. Since Blough's procedure takes into account the possibility of moments of inattention, it might improve the results even with human subjects.

Superimposed on this control of light intensity, pecking had several other effects. Pecks at key B (the stimulus-increasing switch) were occasionally rewarded with a bit of food, and the pigeons were always studied when they were hungry. The rewards were intermittent and irregular, but never given unless the light was actually out. Pecks

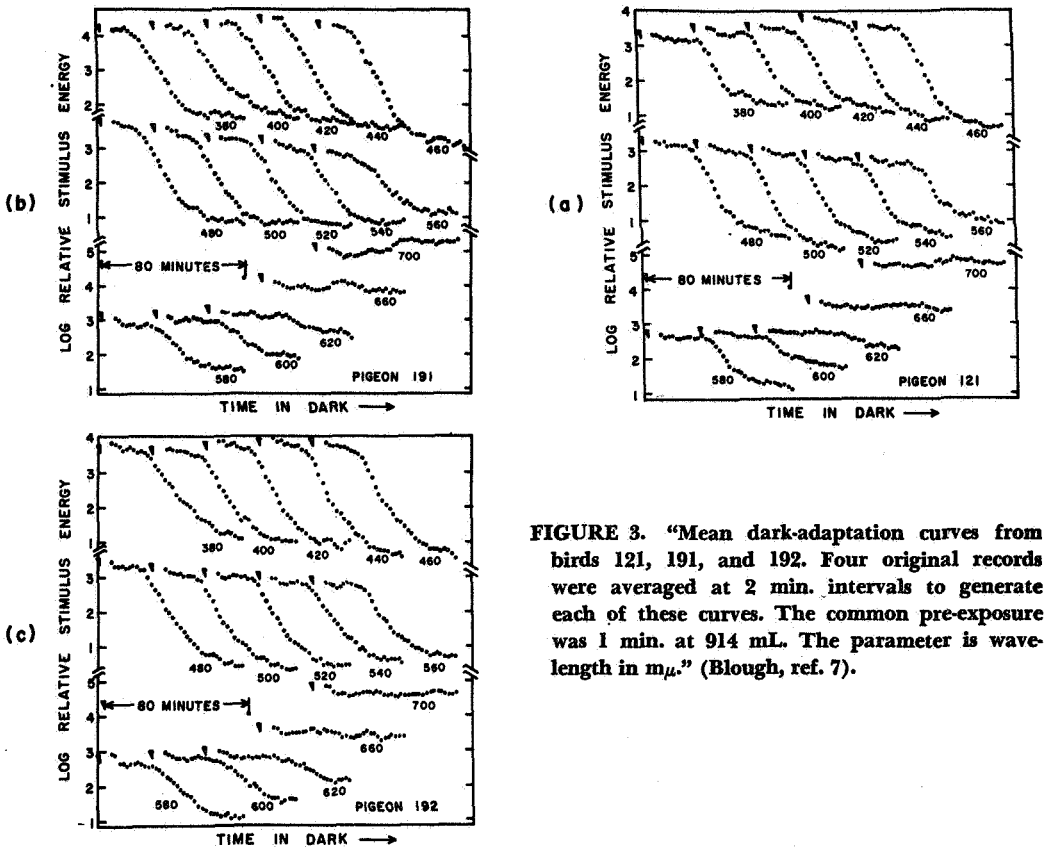

FIGURE 3. "Mean dark-adaptation curves from birds 121, 191, and 192. Four original records were averaged at 2 min. intervals to generate each of these curves. The common pre-exposure was 1 min. at 914 mL. The parameter is wavelength in mμ." (Blough, ref. 7).

at key A occasionally turned out the light by operating the shutter. The shutter closures were intermittent and irregular, but remember that pecks on key A also had a continuous effect on stimulus intensity via the wedge and independent of the shutter action.

Combining the various effects, the procedure made a psychophysical observer out of the subject. Each peck at key A automatically decreased the intensity of the stimulus by 0.03 log unit, and, in addition, occasionally blanked out the light entirely. When the light was actually out, pecks at key B were occasionally rewarded with food. Because both shutter closures and food were given on aperiodic, intermittent schedules, the pigeon was deterred from simply alternating between the two keys without regard to the stimulus. The various schedules were designed so that random alternation would only rarely lead to reward. Pecking at key A drove the stimulus down in small increments, until the pigeon could no longer see the light, which looked to the pigeon like the right time to move to key B. But switching over to key B raised the light intensity above the absolute threshold, and so the pigeon would go back to key A to drive the stimulus down again, and so on. Occasionally, when a key A peck actually closed the shutter, pecks to key B would unpredictably produce the food, but this was relatively uncommon. Most of the time, the

pigeon just switched back and forth between the two keys, as the light dipped down and rose above the threshold. As in audiometry, the subject traces out its threshold as the experimenter varies whatever he is interested in. Blough's actual procedure was even more complicated than I have indicated, for there were slight penalties for incorrect responses and delay contingencies for switching too rapidly from one key to the other, but these are not described here. The foregoing shows amply that the conditions of reward are correlated with the stimulus so that the more fully the subject reveals its sensory capacity the more successful it is in gaining reward.

A sampling of Blough's findings is the best argument for the general method. In one experiment (ref. 7) on three pigeons, he examined the course of dark adaptation for lights of various wavelengths, following preexposure to one minute of white light of an arbitrary intensity. Figure 3 shows the results for the three pigeons, one beneath the other. Each tracing is an average of four runs through the dark adaptation curve, with the wavelength indicated as the parameter. The ordinate is log stimulus intensity on a relative scale, and the abscissa is time. These curves show, first, that pigeons are not unlike people as regards dark adaptation and, second, that Blough's method is a valid way of finding this out. When the stimulus was at the short end of the spectrum, there were clear rod-cone breaks in the threshold, but toward the red end, the rod section disappears, as expected. The first few minutes of each curve are deleted because the pigeons tended to be unstable at the beginning of each session.

From the data in figure 3, Blough constructed the analogues of human photopic and scotopic luminosity functions. The photopic function was taken from the average of the first five data points on each tracing, while the scotopic curve was taken from the

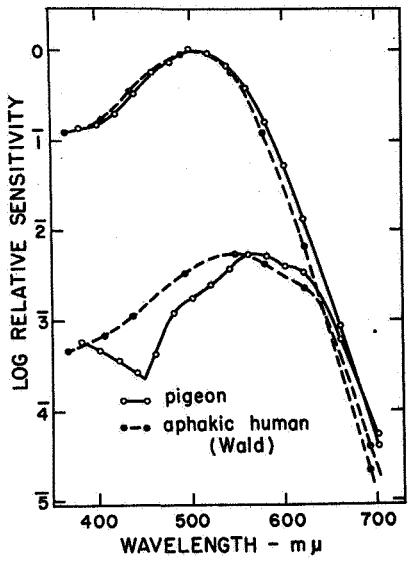

FIGURE 4. "Mean data from Figure 3 plotted together with Wald's spectral sensitivity curves for aphakic human subjects. The human photopic and scotopic curves are independently matched to the pigeon data. Wald's published data have been corrected for calibration errors in accordance with a personal communication." (Blough, ref. 7).

average of the last five points. These are shown as reciprocals (i.e. sensitivity instead of stimulus intensity) in figure 4, which also plots Wald's (ref. 8) data for human subjects who lack lenses (aphakics) to take account of the pigmentation of the human lens. The two sets of data agree to a fair extent, but it should be noted that the scotopic and photopic curves were matched independently, so that the figure contains no information about the scotopic-photopic separation (the "achromatic" interval). Finally figure 5 shows the agreement between Blough's data on the one hand, and, on the other, Granit's (ref. 9) and Donner's (ref. 10) electrophysiological data for the pigeon eye. The physiological data plot the firing of retinal elements in the pigeon eye, using a given level of nervous activ-

ity as the criterion of response. The response was obtained as the wavelength of the incident light was swept back and forth through the visible range. At each wavelength, the minimum intensity for the criterion response is plotted. Donner used a dark-adapted eye, while Granit used a light-adapted eye, so that their data are, respectively, applicable to scotopic and photopic processes. Once again, the size of the achromatic interval cannot be taken as equal since the curves were matched independently. The agreement nevertheless further indicates that Blough's psychophysical method reveals something about the visual process itself and not just the accidents of the training procedure.

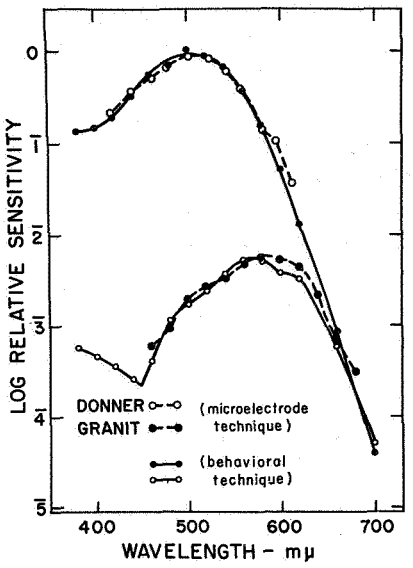

FIGURE 5. "Mean data from Figure 3 plotted together with electrophysiological threshold data on the pigeon eye obtained by Granit and by Donner. The electrophysiological curves are independently matched to the behavioral curves." (Blough, ref. 7).

SENSORY MAGNITUDE

The study of sensation has long sought a quantitative measure of psychological magnitude. We start by knowing, for example, that some lights appear to be brighter than others, and also that, in general, the appearance depends on the physical energy. But we also know that physical measures rarely predict psychological magnitudes in quantitative detail. For most of man's modalities, the sensory intensity is non-linearly related to the physical measure of the stimulus, but psychologists try to describe the non-linearity more exactly. After about a century of thinking that sensory magnitudes are logarithmic functions of physical intensity (ref. 11), we now have reason for believing that the general relation is a power function, with various exponents for the various modalities (ref. 12). For example, psychological brightness in vision is proportional approximately to the cube root of luminance for man. In contrast, loudness is proportional to the 0.6 power of sound pressure. Taking all modalities, the exponent ranges broadly, the known maximum being for the sensation caused by an electric shock to the skin, for which sensory magnitude grows as the 3.5 power of the current passing through the finger. These exponents are established in experiments that require human observers to make judgments relating to the intensity of their sensations. Sometimes the observer is asked simply to say numbers proportional to his sensations as the stimulus is varied by the experimenter; sometimes he is asked to adjust the stimulus intensity himself, until it seems to be in a given ratio to an arbitrary stimulus; sometimes he is asked to match the ratio of the apparent intensities of one pair of stimuli to that of a given pair, and so on. In general, the observer's task is to respond overtly in some way proportionate to the sensory magnitude. Can this sort of experiment be done with animals? Must we teach animals about ratios and proportionalities to find out how intense stimuli seem to them?

The experiment described below yields some information about the apparent magnitudes of sensation in pigeons, without having imparted any mathematical sophistication to them.

Van Sommers and I (ref. 13) were trying to learn something about the pigeon's experience of visual brightness, in particular whether it obeyed the power law, the logarithmic law, or, more fundamentally, whether such a question can be asked sensibly of a pigeon. As usual, the pigeons were hungry and were trained to peck at a key for food reward. In this experiment, however, pecking was rewarded if and only if it occurred at a certain rate, defined by the duration of the inter-peck interval. For example, the pigeon got fed when two consecutive pecks were no more than 11 and no less than 10 seconds apart. A premature or tardy peck got no food and restarted the interval. Pigeons on this procedure are known to be able to conform roughly to the required rate, tending on the average to respond a bit too quickly. However, because their responding remains somewhat variable in rate, they continue to receive occasional rewards notwithstanding the tendency to speed.

In our experiment, the pigeon's task was further complicated by an imposed correlation between the visual stimulus and the required rate of responding. When the light (which was projected directly on the response key) was bright, a high rate of responding was called for; when it was dim, a low rate was required. In between, medium intensities were correlated with intermediate requirements. All in all, there were five "training" intensities correlated with five required rates of responding, picked so that brighter lights called for faster pecking. The stimulus intensities covered a range of 2.4 log units with a stimulus every 0.6 log unit, while the corresponding required rates of responding were from about 0.7 to 0.005 responses per second. Expressing these as inter-peck durations (which are the reciprocals of the rate), the pigeons were required to peck at intervals of about 1.4 seconds for the brightest light and of about 200 seconds for the dimmest, with three intermediate values for the three stimuli in between. To be rewarded, the response had to fall within $\pm$ 5 percent of the required interval. As noted above, the responses tended to be premature. The size of acceptable range around the required interval is the main way to control the frequency of reward—the broader it is, the higher the proportion of rewarded responses. The ideal frequency of reward is the minimum which sustains performance, for then the animal is satiated with food most slowly and is not likely to rely on reward itself as the distinguishing feature among the five training stimuli and the four "test" stimuli, the latter to be described below.

During each experimental session, the stimuli came on at irregular intervals and in an irregular order. After sufficient practice, the pigeon's responding adjusted rapidly to whatever stimulus was presented, shifting its rate up or down as required. At this point, the test stimuli were added to the procedure. The four test stimuli were intensities falling at the geometric centers of the intervals between the five training stimuli. Since the training stimuli were separated by 0.6 log unit (6 dB in fig. 6), the tests were always 3 dB from the adjacent training stimuli. The presentation of test stimuli was randomly interspersed among the training stimuli. A test stimulus stayed for variable periods of time, during which no responses were rewarded. However, as noted, the generally low rate of reward kept the absence of reward during tests from becoming distinctive.

The main result of the experiment (see fig. 6) was the responding to the test stimuli,

enclosed by squares in the figure. The required rates of responding are shown by the hatched functions in the figure ("training curve"). The rates of responding actually obtained to the training stimuli are at 0, 6, 12, 18, and 24 dB for each pigeon. The rates to the test stimuli are at 3, 9, 15, and 21 dB. In each of the eight cases (four for each pigeon), the rate of responding to the test stimulus fell between the rates to the two adjacent training stimuli, even though the pigeons were never rewarded at all during the tests, let alone for these rates. Responding to the test stimuli must, therefore, have had something to do with how bright the lights looked to the pigeons. It can be shown mathematically that the logarithmic law predicts that the responding to the test stimuli, which are each at the geometric center of a training interval, should be at the arithmetic mean of the responding to the adjacent training stimuli. However, the power law predicts responding at the geometric mean. As figure 6 shows, the responding to the test stimuli fell at the geometric means (note logarithmic ordinate), thereby supporting the power function.

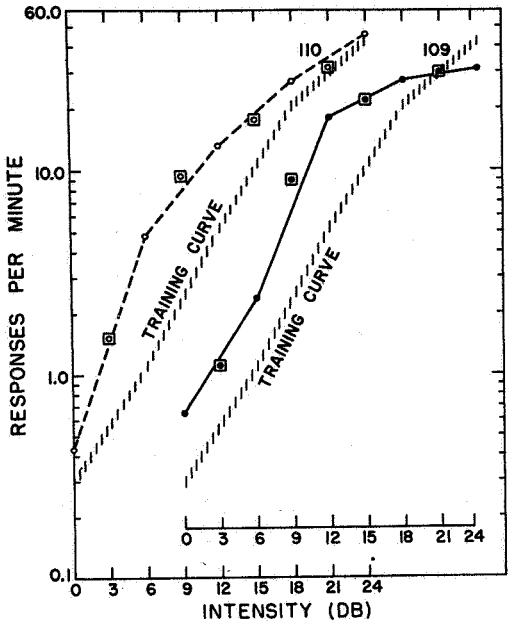

FIGURE 6. "Rate of pecking as a function of the luminance of the stimulus, for two pigeons (Nos. 109 and 110). The training curve shows the prescribed rate of responding at the training stimuli (0, 6, 12, 18, and 24 db). Points enclosed in square give rates obtained with test stimuli (3, 9, 15, and 21 db), in whose presence responding was never reinforced." (Herrnstein and van Sommers, ref. 13).

No doubt, this experiment could have been done more easily with human observers, who could simply have been instructed verbally to respond to the lights. However, there may be occasions when animal observers would be preferable, as, for example, when the physiological basis of sensation is to be studied.

HEDONIC VALUE

Thresholds and magnitudes are by no means the only interesting sensory parameters. Sometimes, we may want to know whether a stimulus is itself rewarding or punishing, not just whether it is detectable or more or less intense. This more purely psychological question, which may be called the question of hedonic value, pervades the contact of animals with their environment. For example, the well-known ability of animals to select a proper diet arises from the hedonic effects of stimuli rather than from the straightforward sensory parameters. The mechanisms of dietary selection are largely concerned with how physiological states are translated into reward and perhaps into punishment. See, for example, Rodgers and Rozin (ref. 14) on thiamine and Krieckhaus and Wolf (ref. 15) on sodium chloride. The translation can take many forms. In some cases, the food is rewarding because of its

nutritive value, but in other cases, the reward is owing to a collateral property of the food, such as its taste. Over the course of evolution, one might expect that such collateral properties would have, at least in some instances, acquired the power to reward. The behavioral effects of sugar nicely exemplify this range of possibilities. It has been shown (ref. 16) that sweetness, independent of caloric content, rewards responding, since saccharine and other non-caloric sweet substances will sustain behavior, at least in rats, and, undoubtedly, human beings. However, it has also been shown (ref. 17 and 18) that at least monkeys and rabbits are somewhat rewarded by the direct injection of glucose into the bloodstream, bypassing the entire ingestive machinery. Other studies (ref. 19) have shown that nutriment at various other points in the physiological chain have some rewarding power over behavior. All in all, it seems that nature is highly redundant in its allocations of the rewarding power of carbohydrates, which is perhaps to be expected given their importance to survival. Other foods and dietary ingredients have also been studied from this point of view, and the tale, though interesting, is far too long for retelling here. My main point is that the study of nutrition is in part a psychological study, centering on the capacity of certain events to control behavior.

No doubt it is obvious that eating involves behavior, for the finding of provender usually requires action. But other contacts between organisms and their environment may also be regulated through the mechanisms of reward and punishment, albeit more subtly. Consider, for example, the diurnal cycle of activity in canaries, which is apparently endogenous as in many creatures. Wahlström (ref. 20) has shown, however, that a canary will, if given a chance, turn the lights in its birdcage on and off to produce a light-dark cycle if the cycle is not externally provided. Then, having produced its own cycle, its general activity waxes and wanes in tempo. The diurnal cycle is not just a passive fluctuation of activity—like the passive fluctuation of air temperature during the 24-hour period—but an active hedonic swing that undoubtedly affects profoundly the animal's natural patterns of life. The distinction is psychological, best studied by behavioral techniques of the type described here.

It may be that such hedonic mechanisms are the rule rather than the exception and that in many physiological systems, the contact between organism and environment is shaped by the dynamic effects of reward and punishment. Van Sommers, for example, has shown (ref. 21) for rats, turtle, and goldfish —representing the three main classes of vertebrate—that respiration involves such a reward system. To pick the intermediate example, figure 7 shows the apparatus devised by van Sommers (ref. 22) to keep a turtle

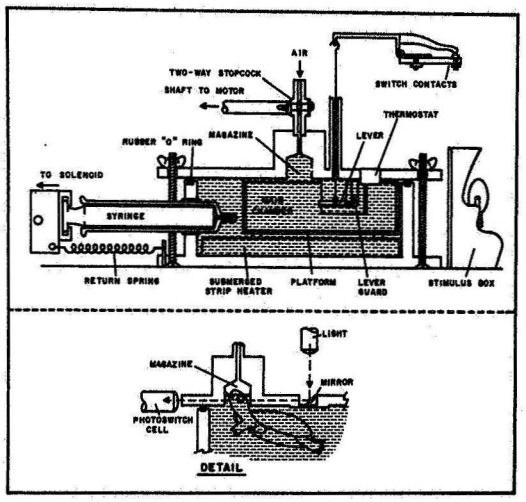

FIGURE 7. "Cross section of turtle apparatus. (Detail: Photoswitch arrangement for recording the entry of the turtle's head into the magazine.)" (van Sommers, ref. 22).

(*Pseudemys scripta elegans*) submerged in water ("main chamber") until a lever was pressed and opened up a small airfilled chamber ("magazine") by operating the syringe and lowering the water level. The first and main point of this study for our purposes is that the turtles did depress the lever and keep themselves adequately ventilated, which is by no means a foregone conclusion. One could imagine an animal whose need for air does not tie into the rest of its effectors so as to permit such adaptability, but the turtle's does. Furthermore, van Sommers found the rate of lever pressing a most flexible instrument of adjustment, for it:

(1) Increased with decreases in the duration of access to air

(2) Decreased with increases in the CO_2 concentration in the air given as reward

(3) Increased with increases in the nutritional richness of the diet (presumably associated with an effect on metabolism level)

(4) Increased with increases in the water temperature (again perhaps associated with metabolism)

And finally, the Q-10 for turtles in the range of temperatures used is a factor of about 2, which approximates the factor by which responding increased for a 10° increase in water temperature.

Contrary to common intuitions (particularly among biologists), it may be that learned responses will prove to be sensitive indicators of physiological states, for local events in the nervous system (such as blood temperature) may affect behavior before the rest of the organism's reactions have taken place. It may, in other words, be misleading to say that in van Sommer's experiments, behavior reflects metabolism, if, in fact, behavior has already begun to restore normal physiological conditions before metabolism has changed materially. Substantial evolutionary advantage would seem to accrue to a creature whose behavior adjusted quickly to the immediate circumstances, both within and around it. But however the physiological details are arranged, van Sommers has shown that respiration in turtles involves more than just breathing: it involves the behavior of the entire turtle, under the control of rewards and punishments. The findings for rats and goldfish were comparable, except that CO_2 regulated the behavior of the mammal and O_2, that of the fish. Here, as in countless other instances, homeostasis extends to the commerce with the external environment, where reward and punishment guide the outcome to produce behavior that is appropriate to the given circumstances. The pattern defines a vast and fertile field of study, as yet largely neglected, no doubt because it falls on the boundary between biology and psychology, but without which both subjects are incomplete.

CONCEPTUAL CAPACITY

The last section moved toward physiology; this one moves in the opposite direction. One may, for example, wonder whether an animal possesses color vision—which is a straightforward question of capacity—or whether its color perception has three, four, five, or more principal colors or whether there is just a simple continuum. None of the procedures so far described are well suited to the latter kind of question, which is more conceptual than perceptual, although this is not to argue for a hard and fast distinction between the two. The problem is to get at how animals sort stimuli that vary in some way and the solution is again to set up contingencies among stimulation, reward, and responding.

A straightforward example of such an experiment was done by Loveland and me (ref. 23), again using pigeons as subjects. We

wanted to know whether pigeons could be trained to detect the presence of people in photographs, for reasons that now have little relevance to our findings. Over the years, many experiments had shown that animals can be trained to respond to the presence or absence of a particular stimulus—a light, a color (given color vision), a geometrical form, a sound, an odor, and so on. All of the procedures described thus far in this paper have relied on such training in one way or another. However, the problem of responding to pictures of people is different from all of these, because the attributes of the appearance of a person are undefined. When we look at pictures, we can see people in a limitlessly large number of different geometrical configurations. People are not fixed geometrical or visual entities, like triangles or red lights, but instances of a class to which we respond without being able to state its properties. A picture may be seen as containing a person whether seen from front, profile, or back, at right angles or obliquely, close up or in the distance, in bright light or dim, with a red tint or green, or with more or less of the body obstructed. A finite list of visual characteristics can give neither the necessary nor all the sufficient attributes. Our experiment with pigeons was thus an attempt to see if such a "natural" class—as distinguished from the contrived stimuli of psychological experiments—can be used as the occasion for responding, and in this respect it seems to have been unique.

The pigeon chamber contained a screen onto which the pictures (35 mm slides) were presented, plus the usual response key to peck at and the standard feeder for giving food reward. Pictures were shown for about a minute at a time and pecking was rewarded with food if the picture contained a person or part thereof. Such correct responding was rewarded only intermittently, so that the reward itself did not become the primary signal that a person was present in the picture. If the picture did not contain a person, then responding was not only unrewarded, but penalized. When the pigeon pecked in the presence of pictures without people, the picture was not withdrawn unless the pigeon had not pecked for at least a certain number of seconds. By responding inappropriately, the pigeon would thus be postponing the removal of pictures in whose presence no reward was given. Without incorrect responding, these negative pictures were automatically withdrawn after about one minute. Each experimental session contained approximately 40 pictures with people and 40 without, presented, of course, in random order.

The pictures themselves were as heterogeneous as we could make them. Some were taken especially for this experiment, in natural settings both indoor and out. Most, however, were just slides that we borrowed or bought from individuals and agencies of one sort or another, taken in all parts of the world, under every conceivable photographic condition, and with an unknown, but likely large, number of different cameras and films. We looked at the pictures ourselves first to determine whether or not they contained people. Then we tested the pigeons.

Within a few weeks of daily practice sessions with a large variety of pictures, the pigeons became highly competent, responding rapidly in the presence of pictures of people, and more slowly or not at all in the presence of pictures without people. The pigeons dealt with the pictures about as accurately as we could ourselves, even pictures they were seeing for the first time. Moreover, their infrequent errors usually made sense if one assumes that they were doing about the same thing a human subject might do with the task. False dismissals—pictures with people, but responded to as if they were without peo-

ple—typically were of hard pictures, which is to say the people in such pictures were obscure, either because of distance, lack of contrast, or some obstruction. However, many such marginal pictures were responded to correctly. False alarms—pictures without people, but responded to as if they contained people—also made sense. Pictures with stimuli that might be taken as people—such as goats or telephone poles in the distance—or objects that are associated with people—such as automobiles or bicycles—were sometimes reported as containing people. Here, too, the general rule was correct performance, but the exceptions were nevertheless revealing and interesting. Then there were, of course, errors that made little sense to a human viewer, except as simple inattention.

This experiment proves that the category of person, which as noted above is not well defined visually, is within the grasp of pigeons—or at least a category sufficiently like person so that a highly mixed set of pictures, both positive and negative by our standards, were correctly sorted. Note, however, that had the pigeons failed, it would not have been because of a sensory deficit in the usual sense. Pigeons are adequately endowed with visual acuity and brightness and color sensitivity to find the people in most of the pictures. As regards visual capacity, pigeons are probably at least the equal of man. Success or failure here depends on some higher level of processing of the stimuli, hence the designation as conceptual. And not only is the level higher, it is also more closely related to the pigeon's natural use of vision than called for in the usual psychological experiment. In nature, as distinguished from the laboratory, stimulus objects representing classes are bound to vary, as they did in this experiment.

We are continuing with experiments of this general type with other classes of stimuli in an effort to find the underlying rule that enables a representative creature, a pigeon, to respond invariantly to highly variable classes of objects. At the same time, we are finding out something about the pigeon's visual world, a possibility that might easily have seemed out of the reach of science a few years ago.

DISCUSSION

QUESTION: What is the degree of complication that you can manage? We have no scale describing complexities.

HERRNSTEIN: We can train pigeons to do some extraordinarily complicated things. Some time ago I thought it would be interesting to see if I could train one pigeon to train another pigeon to stand in the corner. I found that it was well within the animals' range given the appropriate setting. From a practical point of view, for the purposes of studying sensory capacity, the pigeon seems to be quite plastic enough.

QUESTION: What about color perception?

HERRSTEIN: It can be shown that pigeons have color vision and also that they seem to have the principal colors about in the same regions that we do.

QUESTION: What has been done on shape discrimination?

HERRNSTEIN: The last experiment that I described on discriminating human figures in pictures is probably the limiting experiment in the literature since the shape of a person is so complicated that it exceeds our ability to characterize it.

GRIFFIN: Can you give us any specific practical suggestions on how to apply operant techniques to the search for possible "new" or unknown sensory capabilities, such as sensitivity to the Earth's magnetic field?

HERRNSTEIN: The only way to become competent in these techniques short of recapitulating the countless errors that one can make along the way is to work in a laboratory where these techniques are being used.

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Endogenous Timing Factors in Bird Migration

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MIGRATORY BIRDS, in addition to being confronted with problems of spatial orientation, have to solve various problems of orientation with respect to time. The success of their migrations depends, among other factors, upon proper timing of the onset and end of their daily and seasonal migratory activity. The question of which factors are responsible for the initiation of spring and fall migration at the appropriate and specific time of the year has particularly challenged naturalists from the early days of research in this field, and, from the very beginning, opinions were divided between those holding environmental factors responsible and those postulating endogenous factors as principal releasers of bird migrations (e.g., refs. 1 to 7). The former group received strong impetus from Rowan's (ref. 8) discovery that environmental changes in daylength are of overwhelming significance for the timing of migrations in birds. As a result, interest has focussed on this rewarding aspect of the problem, and many bird species have been shown subsequently to depend strongly on environmental changes in photoperiod for the timing of their migratory activities (reviews in refs. 9 to 16).

Photoperiodic induction, however, cannot be the only mechanism, and Rowan himself (ref. 17) in his early papers stressed the fact that the applicability of this concept is obviously limited. Many bird species breeding in the temperate zones migrate to regions close to the equator and thus winter in environments in which seasonal changes in photoperiod are of small magnitude. Nevertheless, these birds depart in spring very precisely at the appropriate time for their homeward migration. Factors other than photoperiod seem to induce migratory behavior in these birds. However, in many equatorial regions, none of the more obvious environmental factors, such as temperature or precipitation, is likely to be the releaser of spring migration because these factors either vary within a narrow range or so irregular that they could not account for the very precise departure of the birds. It has been speculated, therefore, by Rowan and others that these birds may be equipped with an endogenous timing mechanism that makes their temporal orientation independent of environmental information (e.g. refs. 18 to 22). This paper reports experiments carried out to test this hypothesis. The results revealed that en-

[1] Previously unpublished investigations on *Zonotrichia* reported herein were supported by a grant from the National Science Foundation (GB–5969X) to Professor D. S. Farner.

dogenous stimuli are, in fact, essential timing factors in warbler migration, not only for the initiation of migrations at the appropriate times of the season, but possibly also for the termination of migration at the appropriate places.

GENERAL EXPERIMENTAL PROCEDURE

The subjects of most of the experiments summarized in this paper are two closely related species of the old-world warbler genus *Phylloscopus*. The willow warbler (*P. trochilus*) is a long-distance migrant with breeding grounds throughout most of the palaearctic region and winter quarters in equatorial and southern Africa. Its sibling species, the chiffchaff (*P. collybita*), on the other hand, is a short-distance migrant, breeding in the more southwesterly parts of the palaearctic and wintering in the Mediterranean area. Only a few individuals of the western races seem to cross the Sahara on their migrations. (These migrations are covered later in detail.)

All the birds employed in this study were taken from their nests in southwestern Germany and in northern Sweden and raised by hand. After they had reached independence they were housed individually in 42 × 28 × 23 cm registration cages in which their locomotor activity was recorded on event recorders by means of miniature switches mounted underneath one of the perches. By this method it was possible to obtain a continuous record on "Zugunruhe," the nocturnal activ-

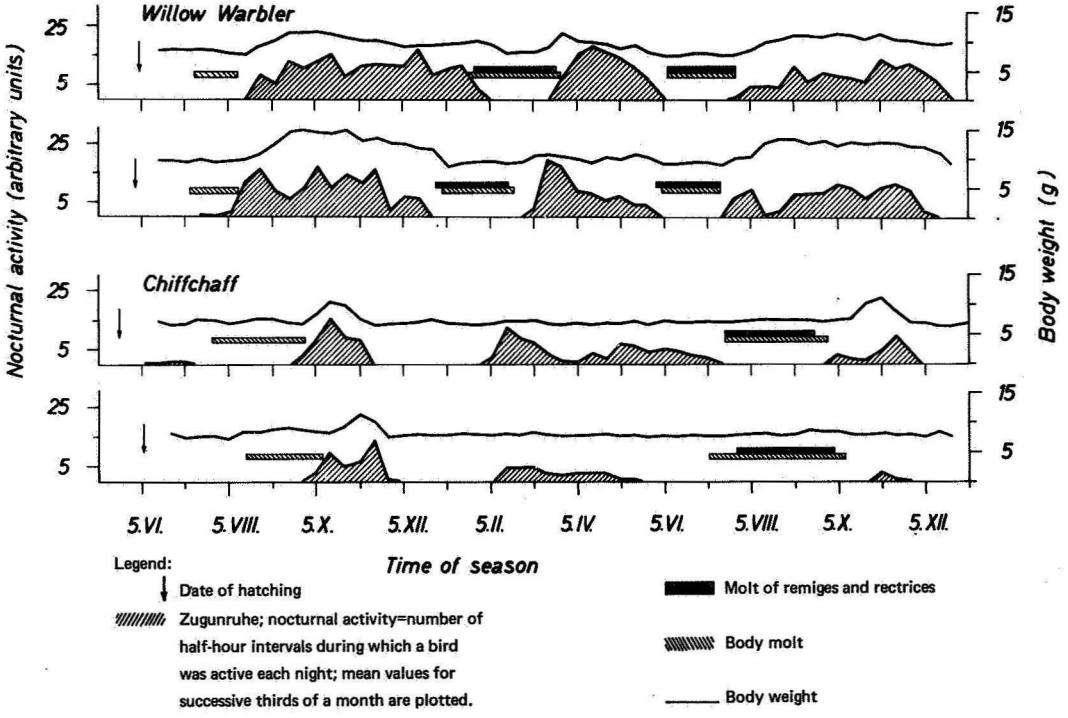

FIGURE 1. Variations in Zugunruhe, body weight and molt in two willow warblers and two chiffchaffs kept under natural photoperiodic conditions of their southwest German breeding grounds.

ity, typically shown by nocturnal migrants during the migratory seasons (ref. 23). In addition, body weights and data on molting were taken at regular intervals, usually twice a week (for details see refs. 24 and 25). Birds were kept in the following experimental conditions:

(1) ENi: Natural photoperiodic conditions of the southwest German breeding grounds in Erling (48°N, 11°11′E), in a temperature-regulated room (21° ±2°C)

(2) B: Natural photoperiodic conditions of the central African wintering area of the willow warbler in Bukavu, Congo (2°4′S, 28°39′E), either outdoors or indoors in a temperature-regulated room (23° ± 2°C) with large windows

(3) *LD 12*:12 and *LD 18*:6: Constant artificial photoperiodic conditions with 12 and 18 hr of light, respectively, in 24 hr (200: 0.02 lux unless otherwise noted), in temperature-regulated chambers (20° ± 1°C or 23° ± 1°C)

The usefulness as well as the limitations of this indirect approach can be illustrated by results obtained from willow warblers and chiffchaffs kept for a period of about 9 months under natural photoperiodic conditions of their breeding grounds. The representative examples, depicted in figure 1, show that the behavior of the caged birds reflects fairly accurately the normal annual cycle of the two species. The birds perform nocturnal activity during the migratory seasons, accompanied at least in autumn by an increase in body weight typical for most migratory birds. Periods of Zugunruhe and obesity are separated by periods of molt. As in freeliving birds, postnuptial molt is complete in both species; prenuptial molt, on the other hand, is complete only in the willow warbler, whereas only a few of the chiffchaffs replace parts of their body plumage.

Despite this harmony in general features between the behavior of caged birds with that of freeliving conspecifics (some other characteristic differences between the species will be discussed below), discrepancies appear in some important details. For instance, obesity, typical for both species during autumn Zugunruhe, is nearly absent in spring, whereas freeliving individuals apparently become as fat in spring as in autumn. More importantly, spring Zugunruhe is extended in both species beyond the date at which actual migration stops, continuing until the onset of postnuptial molt. While we can only speculate on the reasons for such discrepancies, these findings indicate obvious weaknesses of the method employed and thus suggest caution in the interpretation of the results.

RESULTS

Initiation of Zugunruhe in Seasonally Constant Conditions

Spring.—A first series of experiments was carried out to investigate whether or not spring Zugunruhe would develop despite the absence of seasonal changes in the environment. Twenty-five willow warblers from southwestern Germany were hand raised in the springs of 1966 and 1967, respectively, and kept until autumn under the natural photoperiodic conditions of their breeding grounds. Between September 18 and 21, when most individuals had started to exhibit autumn Zugunruhe, they were divided into four groups and transferred to the following experimental regimes: Group I remained under the natural photoperiodic conditions of their breeding grounds; group II was displaced by air to a location in central Africa within the winter range of the species; groups III and IV were transferred to constant photoperiodic conditions with 12 and 18 hr of daylight, respectively, per 24 hr.

Figure 2 shows that Zugenruhe develops in the birds of all experimental groups. It is preceded, in all birds, by prenuptial molt and followed by postnuptial molt in those birds kept long enough under experimental conditions.

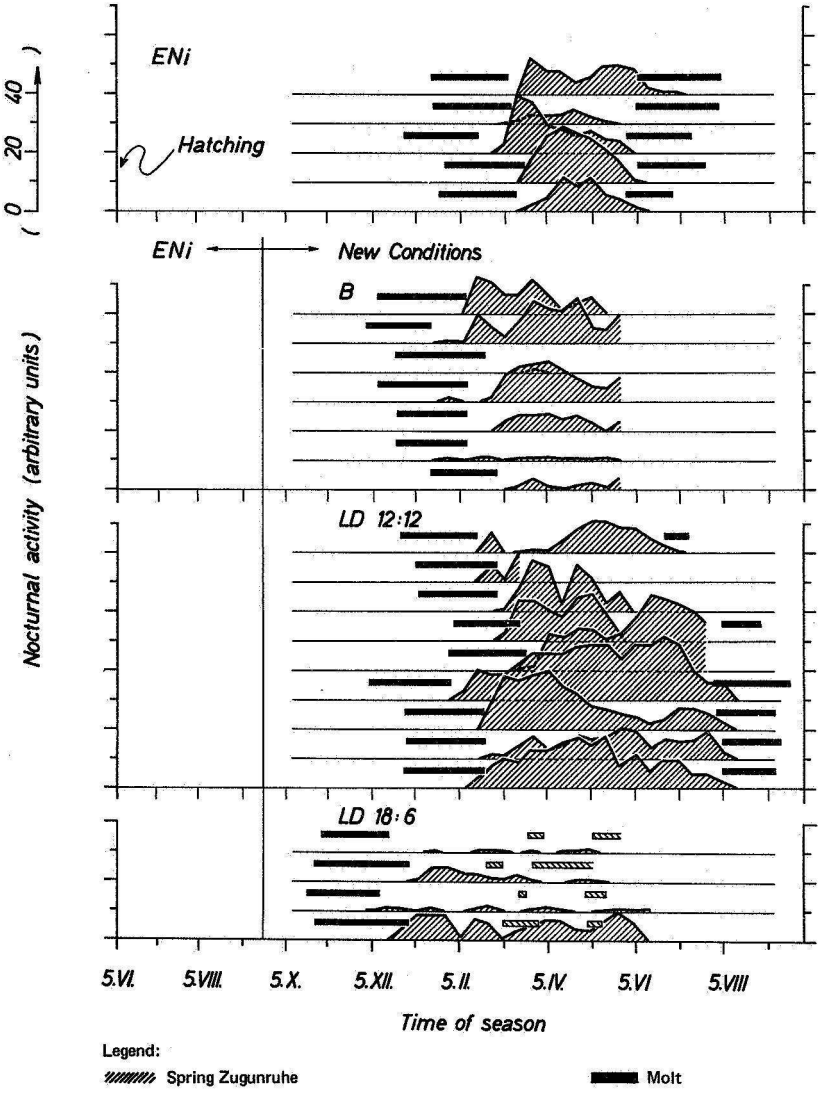

FIGURE 2. Spring Zugunruhe and molt of willow warblers kept under natural photoperiodic conditions of their southwest-German breeding grounds (ENi, upper graph) and from birds transferred between September 15 and 20 from such conditions to either of the following schedules: *LD 12*:12, *LD 18*:6 = constant 12-hr photoperiod or 18-hr photoperiod, respectively. B = natural photoperiodic conditions of a location (Bukavu) within range of central African wintering grounds of the species (either outdoors—upper 3 birds—or indoors). For further explanations, see figure 1.

Apart from differences in timing, no major differences in the behavior of the birds kept in *LD 12*:12 and those living in natural light conditions can be detected. The willow warblers kept in *LD 18*:6, on the other hand, behave abnormally in at least two respects. Zugunruhe is weak in most subjects and is frequently interrupted or superimposed by short periods of body molt.

These results clearly demonstrate that spring Zugunruhe as well as pre- and postnuptial molt can occur independently of seasonal changes in photoperiod and temperature. Furthermore, the fact that the events investigated occur at different times of the season, depending on the experimental conditions, suggests that these processes are governed by endogenous factors rather than by uncontrolled environmental stimuli penetrating the experimental chambers.

Autumn.—A second set of experiments was conducted to test whether the same behavior pattern would hold for fall Zugunruhe and the events preceding and following it. Twenty-four willow warblers were taken from the nest at an age of 6 to 11 days and transferred immediately to a constant 12-hour day and 18-hour day, respectively. They were kept there until January of the subsequent year. The behavior of these birds was compared to that of a control group living under the natural light conditions of their breeding grounds.

Figure 3 summarizes the essential results. It is obvious that Zugunruhe develops in an orderly manner in all birds, regardless of the conditions under which they are kept. Similarly, postjuvenile molt is carried out by all individuals. Prenuptial molt, on the other hand, can be observed only in the birds kept under natural light conditions or in *LD 12*:12, but not in the long-day group. Since the long-day conditions delay postjuvenile molt as well as Zugunruhe, the experimental

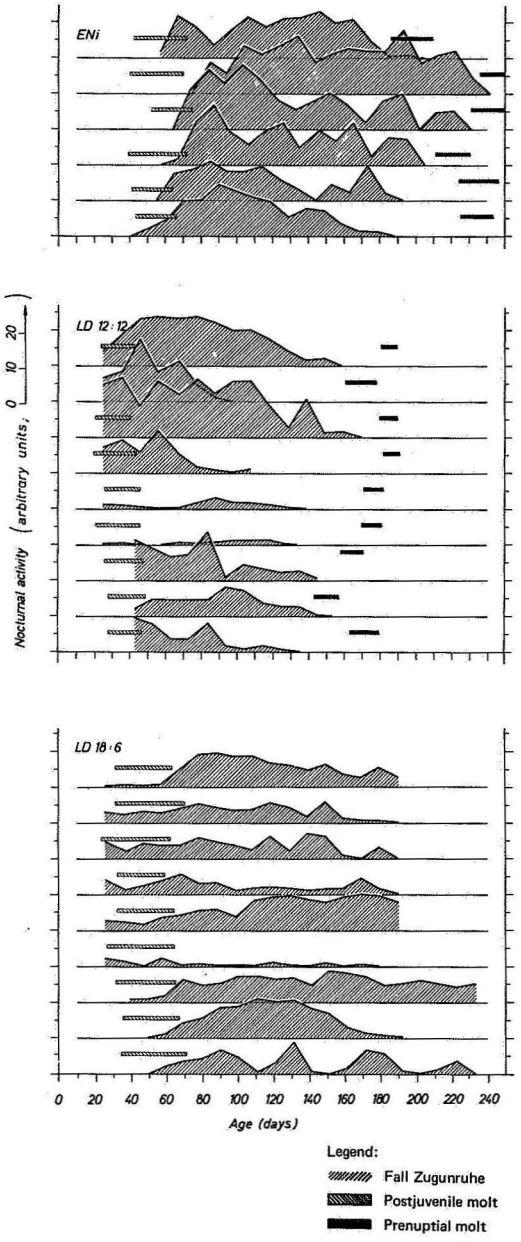

FIGURE 3. Fall Zugunruhe, postjuvenile molt, and prenuptial molt of birds raised from an average of 9 days either indoors under natural photoperiodic conditions of their breeding grounds (ENi) or in a constant 12-hr or 18-hr photoperiod. For further explanations see figure 1.

period may have been too short for prenuptial molt to occur.

In birds kept under natural light conditions, intense nocturnal activity usually sets in when postjuvenile molt is almost completed. Therefore, I did not start to record activity in the experimental bird until they had begun to molt. As it turned out, however, Zugunruhe was already intense in most of the birds kept under constant light conditions at that time. For that reason the exact times of onset of nocturnal activity are unknown in most of these birds.

Even though the results described in this section are not as unequivocal as those obtained from the experiments described before, the conclusion is justified that one group of factors controlling the onset and end of pre- and postnuptial molt as well as of the onset and end of Zugunruhe is within the bird.

The nature of the time measuring mechanism.—The results discussed so far are not sufficient to come to any definite conclusions about the nature of the postulated endogenous mechanism. Theoretically, two possibilities have to be considered:

(1) An hourglass type mechanism, i.e., a time measuring device which has to be set at least once a year by environmental stimuli

(2) A rhythmical process with a period of about one year which continues to oscillate for at least several periods even in the absence of periodic environmental stimuli. To decide between these two alternatives it was necessary to keep warblers for more than one year in seasonally constant conditions.

Results of such experiments have been described in detail elsewhere (refs. 24 and 25).[2] They all clearly favor the endogenous rhythm hypothesis. As an example, figure 4 illustrates the behavior of two willow warblers during a 28-month period in *LD 12*:12. It can be seen that both birds continue to molt twice a year; in between the molts they develop Zugunruhe. Moreover, the phases of the molt and Zugunruhe cycle in bird *a* (left) shift progressively forward, thus expressing a freerunning rhythmicity with a period length of about 10 months. In bird *b*, which is a sibling of bird *a* and which was kept in a cage adjacent to that of bird *a*, the average period length is close to 12 months. This deviation of the period length from the 12-month periodicity in the environment definitely excludes the possibility that uncontrolled exogenous stimuli may have caused the rhythm; it must be endogenous.

The results presented in the last three sections provide answers to our initial questions. Zugunruhe and molt in the willow warbler are controlled by an endogenous annual rhythmicity which may persist for at least three cycles under constant environmental conditions. As in the few other animals for which the existence of such circannual rhythms has been demonstrated (refs. 26 to 33),[2] its most obvious function is that of the timing of biological events. The following sections show, however, that circannual rhythms might be much more basically involved in the control of migratory behaviour in warblers.

Experiments on the Termination of Zugunruhe in Autumn

A substantial body of circumstantial and experimental evidence suggests that birds travelling to their winter quarters for at least the second time in their lives find their goal through goal orientation. Some inexperienced first-year birds, on the other hand, have been demonstrated to be capable of direction orientation only (reviews in refs. 34 and 35).

[2] BERTHOLD, P.; GWINNER, E.; AND KLEIN, H.: Circannuale Periodik bei Grasmücken (*Sylvia*). Experientia, vol. 27, p. 399.

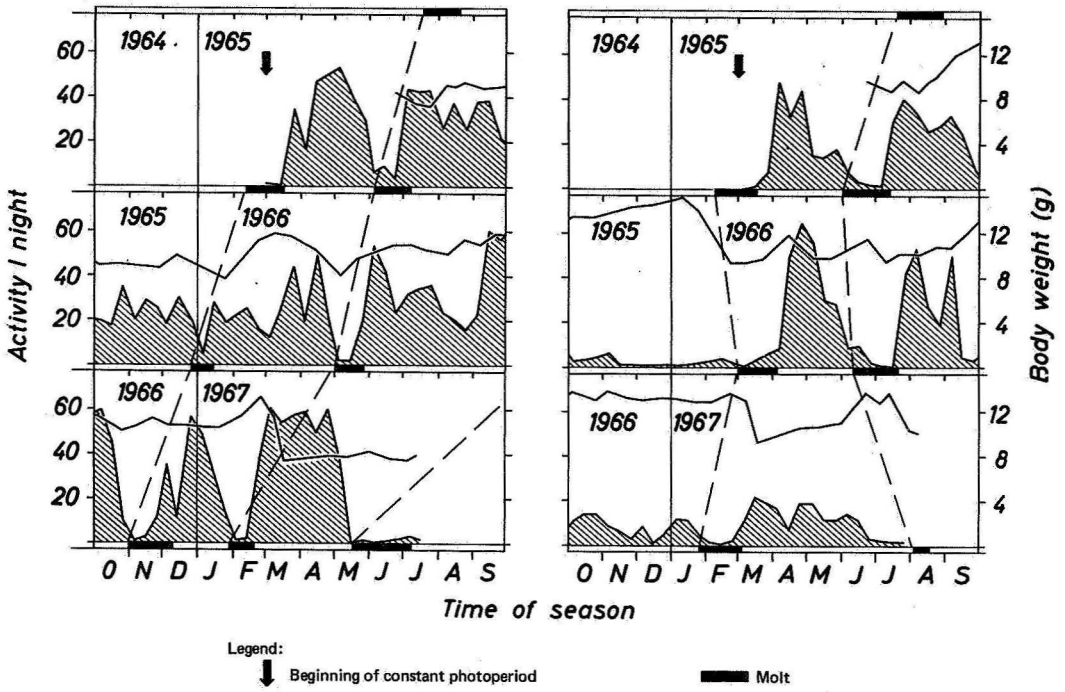

FIGURE 4. Variations in Zugunruhe, body weight and molt in two willow warblers kept from late February 1965 for 27 months in constant 12-hr photoperiod (200 : 0.2 lux) Successive years are displayed below each other. Dashed lines connect onsets of corresponding molts in successive years. Activity per night = number of 10-min intervals during which a bird was active each night; mean values for successive thirds of a month are plotted. Other symbols as in figure 1 (ref. 24).

While, in the case of goal orientation, the orientation mechanism by definition contains a component that guarantees termination of migration upon arrival, such a component is lacking in the case of direction orientation. This poses the problem of what factors are responsible for the termination of autumn migration in birds capable only of maintaining a given direction. At least three mechanisms are conceivable:

(1) The birds may have an innate knowledge of the environmental features of their winter quarters.

(2) The birds may have an innate knowledge of the distance they have to travel.

(3) The birds could have an innate knowledge of the time they have to travel with a given average speed.

There is little evidence on which to decide which one of these mechanisms might be involved. Results of some experiments (refs. 36 and 37) have been interpreted as supporting (1), but in no case is this conclusion convincing (refs. 24 and 37 to 39). Other findings suggest that endogenous mechanisms, (2) or (3) above, are involved (e.g., refs. 40 and 41). The following sections summarize some pertinent experimental results.

Autumnal displacement of willow warblers to central Africa.—The main objective of the autumnal displacement of young willow warblers directly into the central African

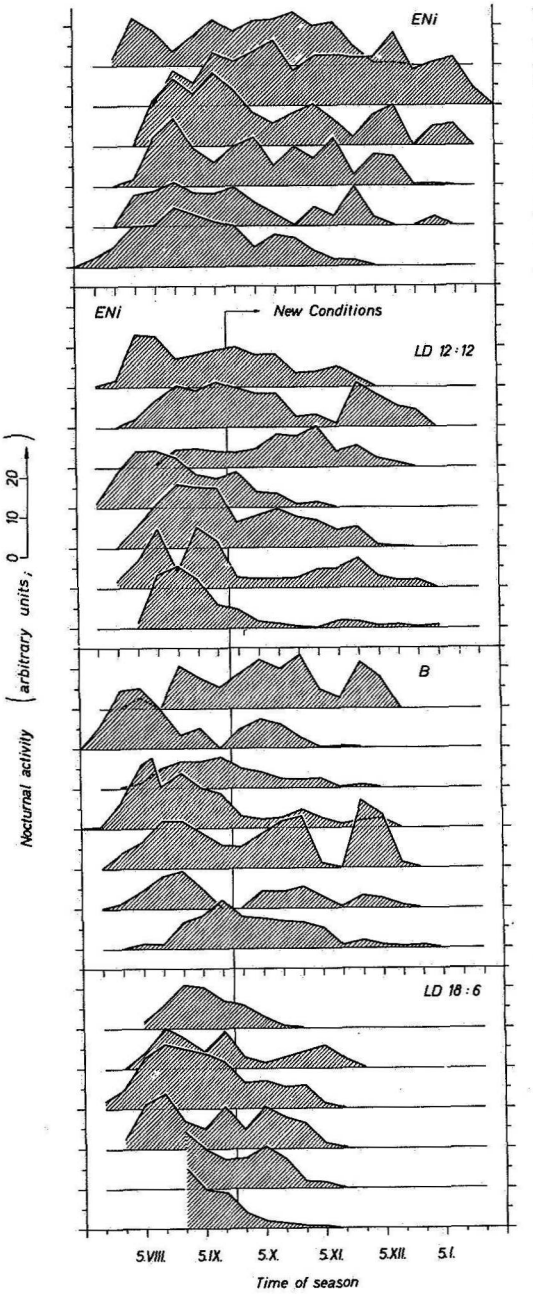

FIGURE 5. Fall Zugunruhe in willow warblers kept under natural photoperiodic conditions of their southwest-German breeding grounds (ENi, upper graph) and from birds transferred between September 15 and 20 from these conditions to either of the following experimental schedules: *L*D 12:12, *L*D 18:6 = constant 12-hr and 18-hr photo-period; B = natural photoperiod conditions of a location (Bukavu) within the range of the central African wintering grounds of the species (either outdoors: upper three birds, or indoors). For further explanations see figure 1.

winter quarters of this species (B in fig. 2) was to test whether environmental factors are involved in the termination of autumn Zugunruhe. On September 18, the date of the displacement, most of the birds had already passed the maximum of their autumn Zugunruhe. By that time, the bulk of free-living willow warblers appears in Africa in regions adjacent to the southern border of the Sahara desert (ref. 24).

Figure 5 and table 1 show that Zugunruhe in all displaced birds continues well beyond the time of displacement. No differences in the pattern, the total amount or the duration of Zugunruhe can be detected, either between the indoor and the outdoor subgroup, or between all of these birds and the controls that had been transferred at the same date to a constant *12*:12 hr day (i.e., to a photoperiod simulating that experienced by the displaced birds). On the other hand, both experimentals and controls differ from the birds transferred to long-day conditions as well as from those retained under the natural light conditions of their breeding grounds. Zugunruhe of the birds of the long-day group tends to cease earlier and to be less intense than that of the experimentals or controls. In contrast, Zugunruhe in the birds kept in natural light conditions of their breeding grounds tends to last longer and to be more intense. Thus, whereas we find no effect of other environmental conditions on duration and intensity of Zugunruhe, we find an effect of photoperiod on these parameters.

TABLE 1.—*Duration and Total Amount of Zugunruhe in Willow Warblers and Chiffchaffs During Their First Autumnal Migratory Season Under the Natural Photoperiod of the Breeding Area (ENi) and After Transfer to Either Artificial Photoperiods (LD) or to the Natural Photoperiod of the Wintering Area (B)*

	Willow warbler			Chiffchaff		
	n[a]	Duration of Zugunruhe (days)	Amount of Zugunruhe[b]	n[a]	Duration of Zugunruhe (days)	Amount of Zugunruhe[b]
ENi	6	137 ± 17.1	1255 ± 342	6	51 ± 22.5	431 ± 272
LD 12:12	7	131 ± 13.7	869 ± 185	8	82 ± 15.2	564 ± 309
B	7	138 ± 11.2	804 ± 268			
LD 18:6	6	85 ± 17.2	675 ± 260			

Legend:
p < 0.001
p < 0.01
p < 0.05

[a]Number of individuals
[b]Total number of half-hour intervals with nocturnal activity during the migratory season

It is clear that these results do not support any hypothesis postulating environmental factors as principal stimuli for the termination of fall migration in willow warblers. On the other hand, they do not exclude such a possibility. Among various possible objections to such a conclusion are the following:

(1) Since it is unknown where the different populations of the willow warbler spend the winter, we cannot be sure whether or not the experimental animals had been displaced to an area in which the critical stimuli prevail.

(2) Even if the birds had been displaced to their population-specific winter quarters, the restrictions of cage life may have prevented them from receiving the appropriate stimuli.

(3) The birds did receive the appropriate stimuli, but cage conditions prevented them from terminating Zugunruhe.

Despite these reservations, it seemed justified and reasonable to look for evidence that might favor one of the alternative hypotheses.

Coincidence between the temporal pattern of Zugunruhe and actual migration. Inspection of figure 5 suggests a rather similar temporal pattern of Zugunruhe in willow warblers exposed to photoperiods of similar duration (i.e., in all birds excluding those of the long-day group). This becomes even clearer if one plots the individual Zugunruhe curves of all these birds on the same graph. Figure 6 indicates a common trend in the temporal course of nocturnal activity. Zugunruhe first increases sharply to reach a maxi-

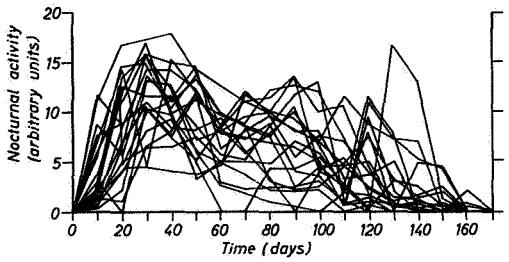

FIGURE 6. Individual Zugunruhe curves of the three groups of willow warblers depicted in upper three graphs of figure 5, drawn over one another. All curves are normalized with regard to onset of Zugunruhe so that they all start at the same point, day 0, on the abscissa.

mum in about 30 to 40 days. Then it steadily wanes and ceases 2 to 4 months later.

This pattern seems to correspond, at least grossly, with the actual pattern of migration. A review of the limited literature on the autumnal passage of willow warblers through southern Europe and Africa reveals that migratory speed is apparently high when the birds cross Europe and northern Africa. The maximal numbers of willow warblers pass through countries just beyond the Sahara only about 4 weeks after peak migration occurs in Europe. Then migration slows down. Rhodesia is reached not before the second half of October and the southern tip of Africa apparently as late as the end of November (ref. 24).

This similarity between the temporal pattern of Zugunruhe in caged willow warblers and the temporal pattern of actual migration suggested the following hypothesis:

(1) It is proposed that the nocturnal activity measured as Zugunruhe in the caged willow warblers is the expression of an endogenous temporal program which determines duration and temporal variations in migratory activity. If this is true then the nocturnal activity displayed by caged birds should be equivalent to a given amount of actual migratory activity, i.e., a given distance travelled by freeliving individuals during the same time.

(2) Furthermore, it is proposed that this temporal program is organized in such a way that it produces just enough migratory activity during the migratory season as is required to reach the goal; that is, the bird will have reached the vicinity of its winter quarters when this program tapers and ends.

The following sections present evidence that indirectly supports this hypothesis.

Comparison of Zugunruhe in closely-related species.—The hypothesis implies that related species or races, travelling different distances on fall migration, develop different total quantities of Zugunruhe during the migratory season. We have tested this prediction by comparing migratory restlessness of the willow warbler with that of its sibling species, the chiffchaff. From the distribution map (fig. 7), one should expect willow warblers to develop at least twice as much migratory activity as chiffchaffs. Figure 8 and table 1 show that this prediction is, in fact, verified. Both in birds kept under natural photoperiodic conditions of their breeding grounds and in birds transferred in mid-September to a constant *12*:12 hr day the willow warblers stay much longer in migratory condition and develop much more migratory activity as the chiffchaffs.

Calculation of the distance equivalent to Zugunruhe.—The hypothesis implies that the amount of Zugunruhe displayed by a caged bird within any given time interval (U_i) is equivalent to the distance D_i traveled during this interval by freeliving conspecifics. The ratio U_i/D_i should then equal the ratio U_g/D_g, where U_g is the total amount of Zugunruhe of the caged bird and D_g the total distance travelled by freeliving conspecifics. U_i and U_g are known. If, in addition, we

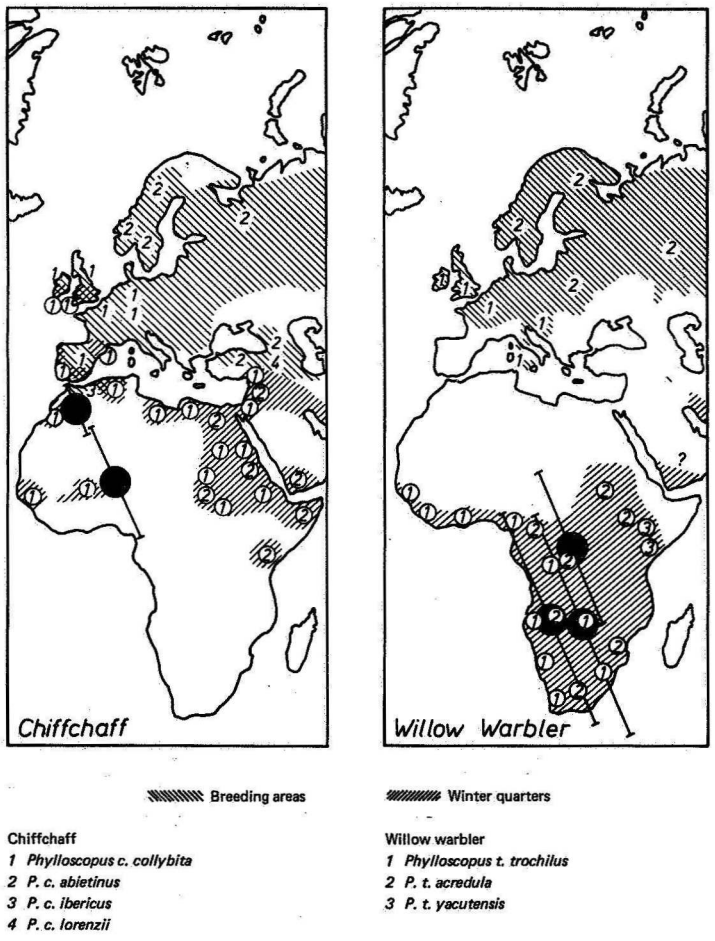

FIGURE 7. Breeding areas and winter quarters of chiffchaff and willow warbler (as in ref. 42). Numbers refer to various races of either species (numbers encircled represent winter quarters). Large solid circles are calculated endpoints of migration (with standard errors) for chiffchaffs and willow warblers kept in three different experimental conditions (as in figure 8. In addition, compare in figure 5 the group of willow warblers displaced to central Africa.).

knew D_i, we could calculate the theoretical distance which is equivalent to the total amount of Zugunruhe of the caged birds using the following formula:

$$D_g = \frac{U_g \cdot D_i}{U_i}$$

If the hypothesis proposed here is correct, this theoretical distance should be approximately that normally covered by the species during migration.

Fortunately such information is available from recoveries of banded birds. While almost no banded *Phylloscopus* warblers have been recovered beyond the Mediterranean Sea, we could get 24 cases of willow warblers and 20 cases of chiffchaffs that had been banded dur-

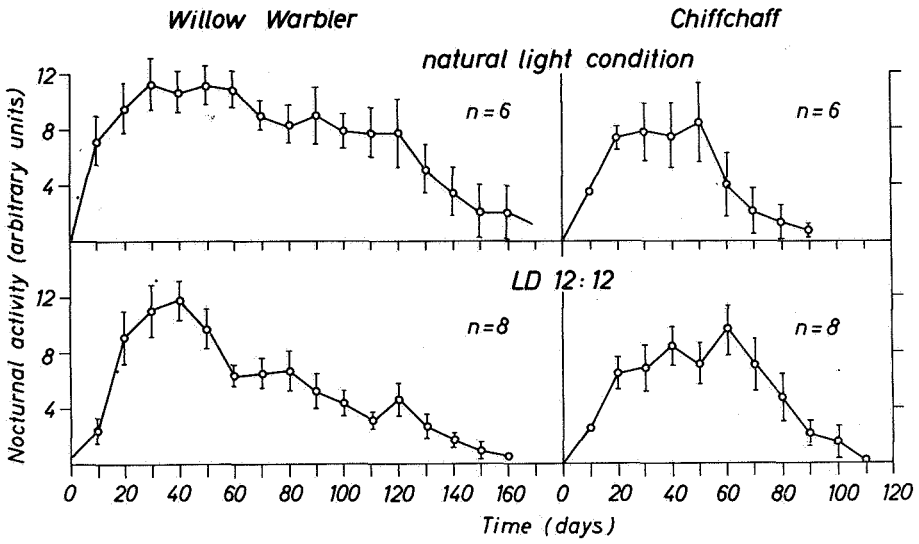

FIGURE 8. Variations in fall Zugunruhe in two groups of willow warblers and chiffchaffs, respectively. Birds were kept either in natural photoperiodic conditions of their breeding grounds over whole period of observation or they were transferred from such conditions to a 12-hr photoperiod. Time of transfer for willow warblers was between days 50 and 80; for chiffchaffs between day 0 and 30. Vertical bars represent standard errors. For further explanations see figure 1 (ref. 43).

ing autumn migration in northern Europe and had been recovered during the same migratory season in southern Europe. From these birds we know, therefore, the distances they have travelled over a given period of time. Using these data, 20 and 24 D_g values, respectively, have been calculated for individual willow warblers and chiffchaffs according to the 20 and 24 D_i values available from banding recoveries. From these, a mean value was calculated for each caged bird. These mean distance values have been averaged again for the 6 to 8 birds of five experimental groups. Then the distance each experimental group would have migrated was plotted on a map under the assumption that the birds would have travelled along the normal migratory route from southwestern Germany to Gibraltar and then south-southeast towards the southern tip of South Africa. Figure 7 shows that the birds would have ended up in their winter quarters.

A better agreement between these calculated distances with those covered during actual migration can hardly be expected since many assumptions had to be made. For instance, the computed distance depends on the time relationship between the onset of migratory restlessness in caged birds and the onset of migration in those freeliving birds from which the distance values have been obtained. For the calculation it has been assumed that both freeliving and caged birds started migratory activity at the same time of the season, but it is not clear to what extent this is true. In addition most of the wild birds which were compared with the caged birds belonged to northern European populations whose migratory pattern might differ from that of birds from southwestern Germany.

Conclusion.—The results and considerations presented so far support the hypothesis that endogenous factors are involved in the termination of fall migration in first-year migrant warblers. Is there evidence that such a mechanism may be significant in other species as well?

Results from displacement experiments with freeliving young autumnal migrants are at least compatible with such an assumption. Rüpell and Shüz (ref. 44) caught first-year carrion-crows (*Corvus corone cornix*) halfway along their migration from the Baltic breeding area to their winter quarters in northern Germany. Birds displaced to a location beyond the actual winter quarters of this population continued to migrate in their original direction. Banded birds were recovered at distances from the point of release not exceeding that which separated them at the point of capture from the southwestern boundaries of their actual winter quarters. Similar results were obtained by Perdeck (ref. 40). He caught starlings (*Sturnus vulgaris*) in Holland on their first fall migration from northeastern Europen to the canal area and displaced them southward to Switzerland and northeastern Spain. Those birds that had started migration comparatively recently continued to travel in their original direction, even if the environment at the release point was favorable for wintering. Only those birds which at the time of capture had already almost terminated fall migration stayed in the vicinity of the release site, provided the release site was in a favorable environment. Perdeck himself (ref. 41) considers endogenous temporal factors as possibly responsible for the continuation of migration in the first group of birds.

Results of a detention experiment conducted by Bellrose (ref. 45) are also compatible with the hypothesis proposed here. Bellrose caught blue-winged teals (*Anas discors*) in Illinois on their first fall migration from Canada to southeastern United States and northeastern South America and detained them until all the adults had passed through. When released, they continued to migrate in the appropriate south-southeasterly direction. An analysis of the data published by Bellrose revealed that recoveries of detained birds were, on the average, from shorter distances than recoveries of birds that had been caught in Illinois but had been released immediately after banding. While about 50 percent of the latter birds were recovered at distances greater than 2000 km from the release site, only about 10 percent of the former were found as far away.

Results from comparative Zugunruhe studies with other birds also confirm the predictions of the hypothesis, at least qualitatively. The upper graph of figure 9 depicts autumnal Zugunruhe curves from two closely related warblers of the genus *Sylvia.* The winter quarters of the garden warbler (*S. borin*) coincide approximately with those of the willow warbler, and those of the blackcap (*S. atricapilla*) are nearly congruent with those of the chiffchaff. Birds were taken as nestlings from the same locations as the *Phylloscopus* warblers and treated the same way. Kept in natural photoperiodic conditions of their breeding grounds, differences similar to those observed in the *Phylloscopus* warblers are found with regard to both amount and duration of Zugunruhe.[3] The autumnal Zugunruhe curves shown in the lower graphs of figure 9 are from members of three races of the White-crowned Sparrow (*Zonotrichia leucophrys*) (Gwinner, Farner and Mewaldt, unpublished data). The birds were caught in their winter quarters and, starting in August, kept in a constant 12-hour photope-

[3] BERTHOLD; GWINNER; KLEIN; AND WESTRIUCK: Unpublished data.

riod. *Zonotrichia leucophrys nutalli* is a year-round resident of California. *Z. l. pugetensis* breeds essentially in western Washington and Oregon but winters in California. *Z. l. gambelii* breeds predominantly in western Canada and Alaska and migrates mainly to the southwestern United States and northern Mexico. On the average, therefore, *Z. l. gambelii* travels a greater distance than *Z. l. pugentensis; Z. l. nutalli* is a nonmigrant.

Since these birds have not been recorded to the end of their Zugunruhe period, no quantitative comparison of duration and amount of Zugunruhe is possible. However, there is a clear tendency in the maximal values of Zugunruhe to increase parallel with the increase of migratory distance.

While in the two *Sylvia* warblers, as in *Phylloscopus*, the temporal pattern of Zugunruhe coincides approximately with the temporal pattern of actual migration, this is surely not the case in the white-crowned sparrows. Even though recording was terminated before the end of fall Zugunruhe, it is clear that it exceeds the time these birds spend on actual migration. Since this is also the case in other short-distance migrants (e.g., refs. 46 and 47), it seems possible that these differences indicate differences in the mechanisms controlling migratory activity in long- and short-distance migrants. In the latter, Zugunruhe may express only vaguely the general readiness of a bird to migrate; the actual time course of its migration may then be molded largely by external factors.

Such a view is supported by the finding, among others, that Zugunruhe in the chiffchaff, the species migrating the shorter distance, is much less rigidly endogenously controlled and probably more susceptible to exogenous stimuli than that of the willow warbler (ref. 48). A stronger dependence on external stimuli of Zugunruhe in short-distance migrants is also suggested by experiments and observations in other birds (e.g., refs. 49 to 52).

The endogenous temporal mechanism proposed here, therefore, may be of dominating significance only in long-distance migrants. Even in these migrants it is probably assisted by other mechanisms. The principal weakness is the mechanism's inaccuracy, and possibly it leads the migrating birds only grossly to the vicinity of their winter quarters where other factors, as yet unknown, determine more precisely where the birds actually terminate migration.

Despite these reservations the evidence presented here strongly suggests that circannual rhythms in warblers and possibly in other migratory birds may be of significance not only for the initiation of migration at the appropriate time but also for the termination of migration at the appropriate place.

DISCUSSION

SLADEN: There is an overlap in your winter distribution. Could the chiffchaffs have exactly the same winter quarters as the willow warblers?

GWINNER: There is an overlap in the winter quarters of the chiffchaff and willow warbler, but apparently not in the winter quarters of the particular races studied (see fig. 7). Recent recoveries of banded warblers confirm such a conclusion.

EVANS: If a migrant normally made a long nonstop flight at some point in its migration, would you expect it to show in captivity, activity levels much greater than average during the appropriate time period? I am concerned particularly with trans-Saharan crossings.

GWINNER: Yes. My hypothesis implies that periods of intense migratory restlessness correspond with periods of intense migration.

EVANS: Are you proposing one synchronization per annual cycle or continual synchronization of the cycle?

GWINNER: I have some results indicating that the circannual rhythms of Zugunruhe, body weight, and molt can be affected by photoperiodic conditions during more than one phase of the cycle. The hypothesis that the annual rhythm of photoperiod

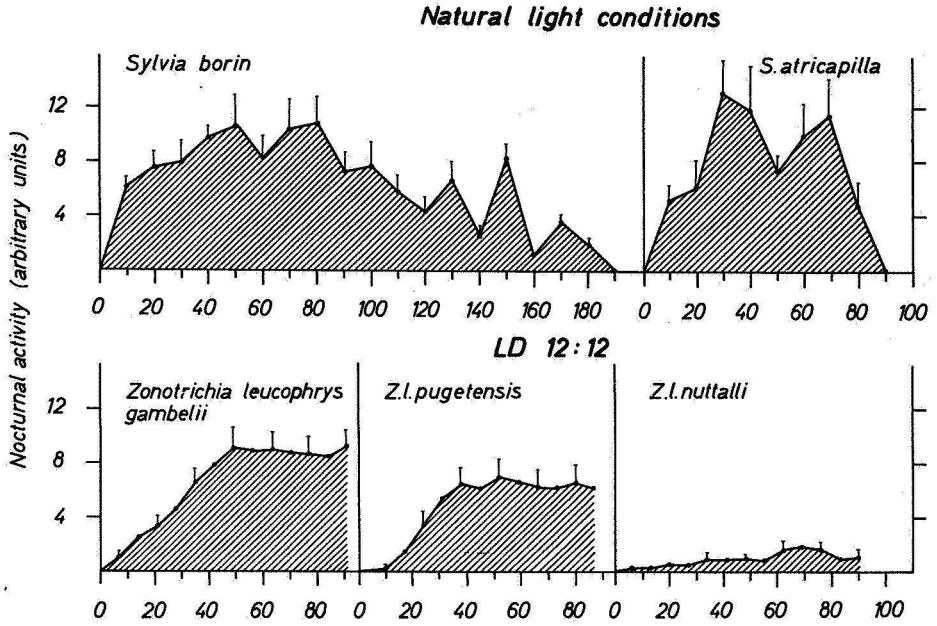

FIGURE 9. Variations in fall Zugunruhe of young garden warblers (*Sylvia borin*) and blackcaps (*S. atricapilla*) under natural photoperiodic conditions of their breeding grounds and of three races of the white-crowned sparrow (*Zonotrichia leucophrys*) kept over the whole period of observation in a constant 12-hr photoperiod (200 lux : 0 lux). Curves are based on mean values of seven garden warblers, seven blackcaps, 20 *Zonotrichia leucophrys gambelii*, 22 *Z. l. pugetensis* and 22 *Z. l. nutalli*. Vertical bars represent standard errors. For further explanations see figure 1.

provides essential stimuli for synchronization has not yet been thoroughly tested, however.

EVANS: Have you tried to determine the influence of food on the level of activity shown during Zugunruhe?

GWINNER: I have only some tentative results indicating that availability of food has little or no effect on Zugunruhe, within obvious physiological constraints, of course. This is in agreement with a variety of other results from experiments with long-distance migrants.

GAUTHREAUX: In your records of nocturnal restlessness do you find periodicity in multiples of 3 days, 4 days, 5 days?

GWINNER: We haven't analyzed the data, so far, under this aspect.

GAUTHREAUX: Have you measured weight changes after a night of very intense nocturnal restlessness?

GWINNER: No, I haven't done that yet. We take body weights usually twice a week. I have no information about short-term fluctuations.

EMLEN: I have noticed that the seasonal sequence of Zugunruhe behavior in caged indigo buntings varies considerably depending upon the conditions of their captivity. In particular, buntings housed in small activity cages approximately 60 × 30 × 40 cm) continued their nocturnal activity long after the normal migration period, while individuals housed in large flight rooms (4 × 3½ × 3½ ft) displayed Zugunruhe activity for a period of only 6 to 8 weeks during the migration season and then such activity ceased. This might be of importance in interpreting your results since many of your graphs show nocturnal activity continuing long after the migration season—until the initiation of the next molt period.

I would also like to comment on the possible importance of seasonal Zeitgebers to circannual rhythms. I have conducted experiments in which

male indigo buntings were maintained for many months under conditions of constant 9- to 11-hr photoperiods. Experiments were initiated following the autumn migration season and results showed that the birds molted, deposited subcutaneous fat reserves, exhibited Zugunruhe, underwent characteristic bill color changes, and initiated song on schedule the following spring. However, the birds did not molt into the winter plumage the following autumn. Although these data are still being analyzed, they suggest an endogenous annual rhythmicity with the additional constraint that the birds require a seasonal Zeitgeber; furthermore, this synchronizing Zeitgeber occurs during the summer or early autumn. This species over-winters in southern Mexico and Central America (roughly 10° to 25° north latitude) where seasonal photoperiod changes are present but minimal. It will be interesting to see what new patterns of circannual rhythmicity emerge as more comparative studies are undertaken.

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SESSION V

Sensory Mechanisms—Mechanical Senses

Chairman, KENNETH D. ROEDER

Neurophysiological Analysis of Echolocation in Bats

NOBUO SUGA
Washington University

In the early 1940's, Griffin and Galambos placed an array of fine wires from the ceiling to the floor of a flight room and studied the echolocating behavior of bats flying across the array. When the bats come close to the array of wires, they increase the rate of sound emission and cross the array. Little brown bats (*Myotis lucifugus*) dodge wires as thin as 0.2 mm (refs. 1 to 3). What part of the brain carries out the most essential processing of the acoustic information necessary for echolocation?

EFFECTS OF ABLATION OF THE INFERIOR COLLICULUS OR AUDITORY CORTEX ON OBSTACLE AVOIDANCE

Cat cortical auditory areas are essential for sound localization. When their auditory cortices are bilaterally ablated, cats lose the ability to localize a sound source (refs. 4 and 5). Since unilateral ablation, however, has little effect on sound localization, the importance of the cortical auditory areas does not depend on information processing—through the corpus callosum—based on interaction between both of the hemispheres (ref. 6). Transection of the corpus callosum and/or the commissure of the inferior colliculus does not affect the ability to localize a sound source (ref. 7). In cats, the most essential cue for accurate sound localization is produced as a result of binaural interaction in the superior olivary nuclei and is utilized only in the presence of the cortical auditory areas.

What part of the bat's brain is the highest center for echolocation? The lower levels of the bat's auditory system, including both the cochlear nucleus and the inferior colliculus, are enormously hypertrophied; but this is not true of either the medial geniculate body or the auditory cortex (ref. 8). Bilateral ablation of the auditory cortex has almost no effect on echolocation across the array of wires (ref. 9). The bat's auditory cortex seems to be less important for sound localization than that of the cat.

Bilateral ablation of the inferior colliculus reduces the ability to echolocate. The effect depends on the extent of the inferior collicular lesion. Figures 1 to 3 illustrate three examples of echolocation after inferior collicular ablation. In figure 1, the dorsal part of the inferior colliculus is bilaterally ablated. The ability to dodge even 0.2-mm wires is

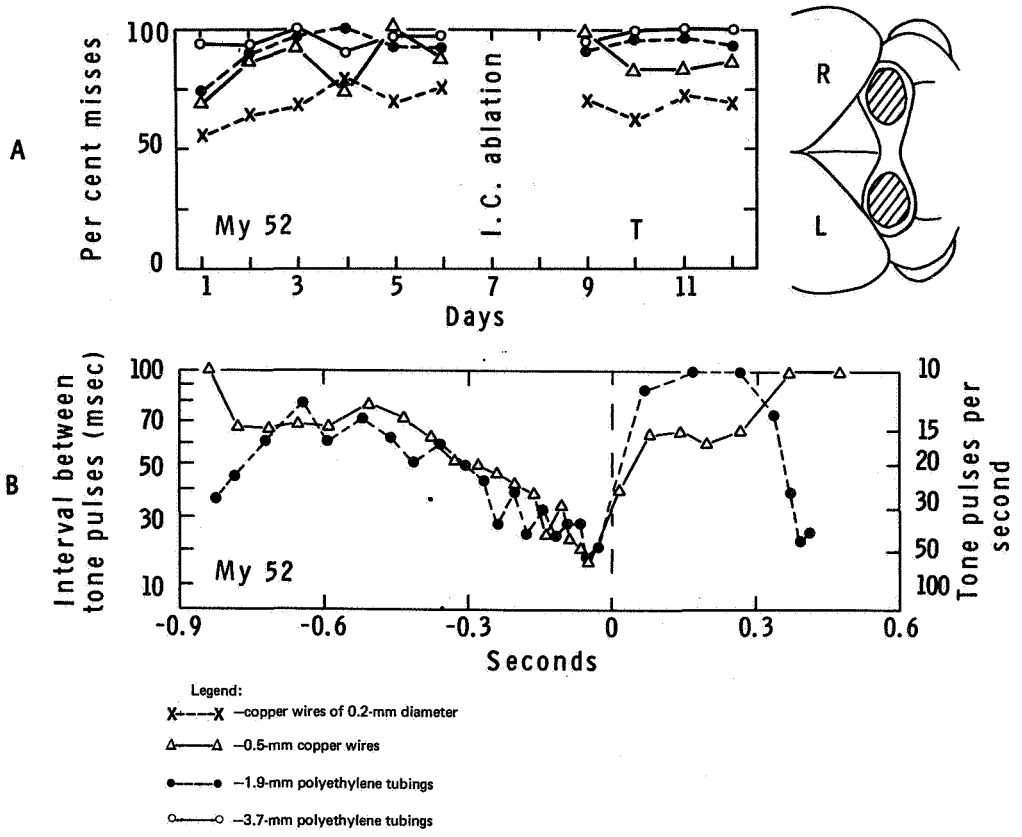


FIGURE 1. Ability to avoid obstacles before and after ablation of the dorsal part of I.C. (A) and rate of emission of orientation sounds during obstacle avoidance (B) of My 52 (*Myotis yumanensis*). In A, ordinate and abscissa represent percent of misses of strands and days since the task of obstacle avoidance was first given to the bat. To the right, dorsal view of mid-brain region is sketched. Shaded areas indicate ablation of I.C. In B, the ordinate represents interval between orientation sounds emitted by the bat in msec to the left and rate of sound emission in tone pulses/sec to the right. Abscissa shows time before and after crossing obstacles in sec. Repetition rate of sound emission increases up to higher than 50/sec immediately before crossing the obstacles. T in A indicates a day on which data presented in B were obtained (ref. 10).

not affected at all, and the change in the rate of sound emission is also normal. Echolocating ability is impaired, however, when the bilateral ablation extends to the ventral part and includes a part of the main nucleus (fig. 2). In this figure the bat always increases the rate of sound emission for wires larger than 0.5 mm at least 0.3 to 0.6 sec before crossing them, although it cannot dodge the 0.5-mm wires. This result indicates that the bat notices the presence of the fine wires, but the analysis of echoes is insufficient in spite of the emission of many orientation sounds.

Very severe unilateral ablation of the inferior colliculus, including a part of the lateral lemniscus, has almost no effect on the

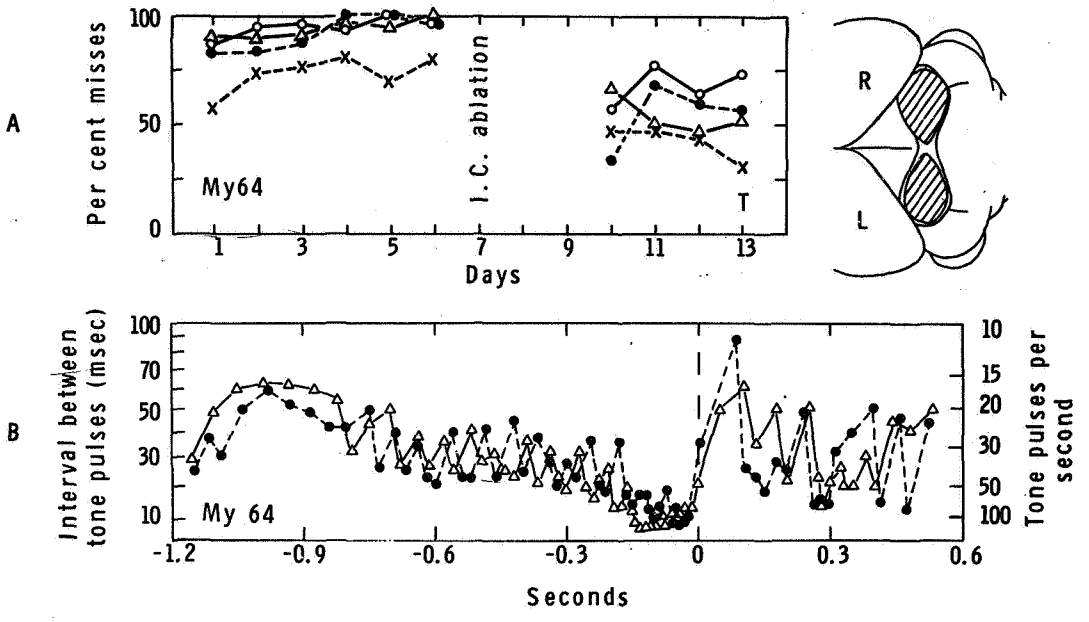


FIGURE 2. Obstacle-avoidance performance before and after I.C. ablation including a part of the main nucleus (A) and rate of emission of orientation sounds during obstacle avoidance (B) of My 64 (*Myotis yumanensis*). Note decrease in percentage of misses (A) and emission of many orientation sounds preceding obstacle avoidance after bilateral ablation of I.C. (B). All symbols have same meaning as in figure 1 (ref. 10).

ability to avoid obstacles (fig. 3). The animal can dodge even 0.2-mm wires. When both of the colliculi are severely ablated, the bat starts to emit orientation sounds at an unusually high rate; but it is unable to avoid even the 3.7-mm polyethelene tubing. The bat shows no signs of obstacle detection and even crashes into the wall (fig. 3). From a series of similar experiments, it has become clear that the main nucleus of one of the inferior colliculi is necessary for processing information essential for echolocation (ref. 10). It is not necessary to compare the activity in the right and left lateral lemnisci or higher auditory nuclei for sound localization.

Information necessary for echolocation is supplied to the inferior colliculus from the superior olivary and cochlear nuclei through the lateral lemniscus. At least two questions about echolocation must thus be considered: what kind of information the inferior colliculus receives from the lower levels of the auditory nuclei and how the information is processed in the inferior colliculus. Neurophysiological data that have been obtained can be reviewed from different aspects such as echo-detection, echo-ranging, echo-localization, and echo-analysis. The following sections are mainly a review of some of the data about echo-detection and echo-ranging.

ECHO-DETECTION AND ELECTRICAL ACTIVITY OF AUDITORY NEURONS IN THE MID-BRAIN

The relationship between ablation, obstacle avoidance, and evoked potential changes

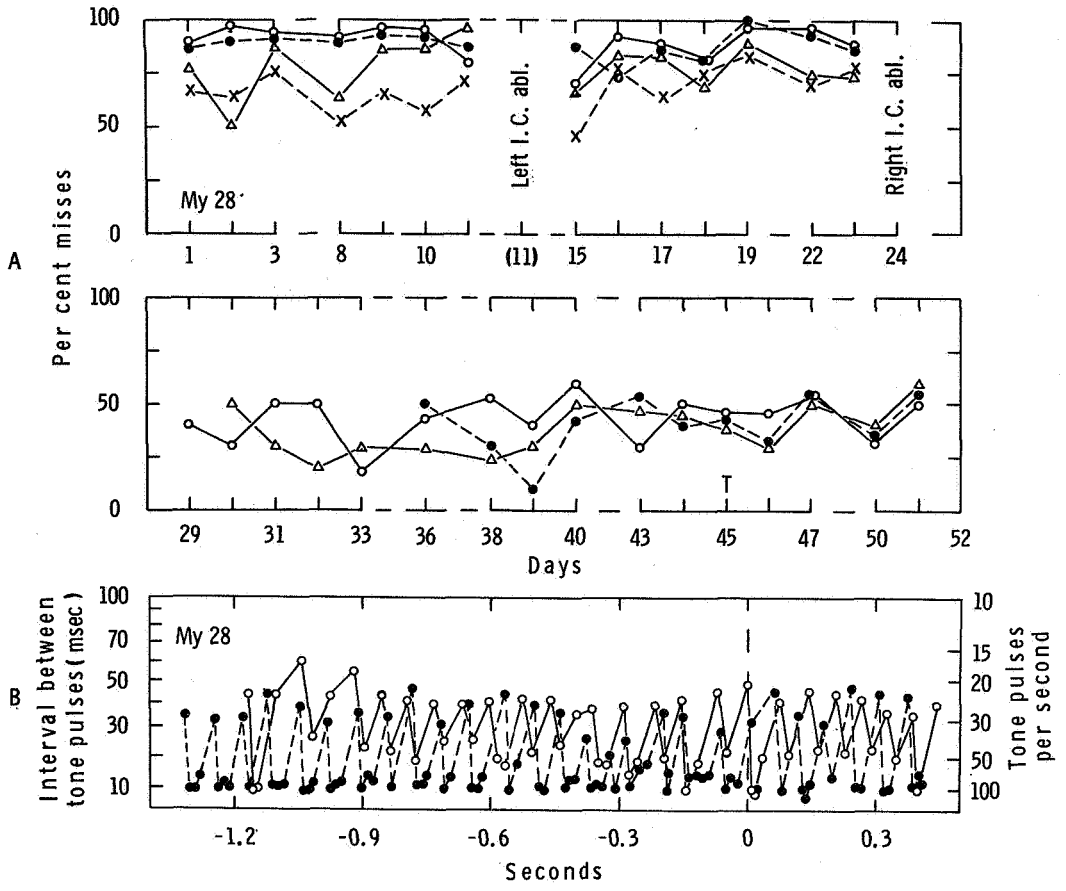
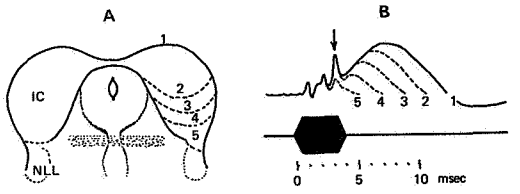


FIGURE 3. Obstacle-avoidance performance before and after severe I.C. ablation (A) and rate of emission of orientation sounds during obstacle avoidance (B) of My 28 (*Myotis yumanensis*). Since severe unilateral ablation of I.C. has no effect on ability to avoid obstacles (upper graph in A), the other I.C. is also ablated severely. Then the bat cannot avoid even the 3.7-mm strands (lower graph in A) in spite of frequent emission of orientation sounds (B). All symbols have same meaning as in figure 1 (ref. 10).

is schematically expressed in figure 4. When a recording electrode is placed on the dorsal surface of the inferior colliculus, two distinct positive potential changes evoked by a sound stimulus of 30 to 50 kHz are recorded. The fast component has a peak latency of about 3 msec, and the slow component has a peak latency of 7 to 9 msec (fig. 4B). Since the bat's brain is small, the summated activity of the auditory nerve and medullary auditory nuclei are often simultaneously recorded as shown in figure 4B. The fast component, called N_4 (ref. 11), mainly represents the summated activity of ascending lateral lemniscal fibers and the slow component represents that of the inferior collicular neurons. The shape and amplitude of these evoked potential changes vary with the frequency and amplitude of the sound stimulus and the location of the recording electrode, because



C. Effect of bilateral ablation of I.C. on echo-location

(1) Avoids even strands of 0.2 mm diameter.
(2) The same as above.
(3) Hits fine strands, but avoids coarse ones.
(4) Hits even strands of 3.7 mm diameter.
(5) The same as above.

FIGURE 4. Schematic presentation of the relation between I.C. ablation (A) and evoked potentials (B). Evoked potentials shown by B1 are recorded with a recording electrode placed on the dorsal surface of I.C. (A1). Certain components of the evoked potentials are, however, affected (B, 2 to 5) by successive ablation of the I.C. from the dorsal side (A, 2 to 5). In B, acoustic delay of the stimulus is corrected. Arrow indicates activity of ascending lateral lemniscal fibers. In C, ability to avoid obstacles after bilateral ablation of I.C. is described. In C, 1 to 5 correspond with 1 to 5 in A and B (ref. 10).

of the tonotopic organization of the inferior colliculus and incoming lateral lemniscal fibers (refs. 10, 12 and 13).

Interestingly the lateral lemniscal (L.L.) evoked potential shows a short recovery cycle and follows repetitive stimuli at a high rate. In other words, the information about echoes coming back from a distance as short as 8 cm is sent into the inferior colliculus. The auditory nervous sytem appears to show adaptation for echo-detection (ref. 14). This adaptation of the auditory system appears to be established between 7 and 10 days after birth. On the fifth day after birth, most of the middle ear cavity is still filled with mesenchyme. The cochlear nerve fiber sends information about repetitive stimuli to the brain at a high rate, but the L.L. fibers cannot convey this information to the inferior colliculus. The L.L. evoked potential shows a long latency—6 msec instead of 3 msec (fig. 5).[1] The nerve fibers in the brain are probably not yet myelinated at this time.

Unlike the L.L. evoked potential, the inferior collicular (I.C.) evoked potential shows a long recovery cycle. The properties of these evoked potentials are very different (ref. 12). This indicates that extensive information processing takes place in the inferior colliculus. In fact, unlike the cochlear nucleus, the inferior colliculus contains various types of neurons. Some of these are specialized for responding to an echo coming back from a certain distance or direction or for responding to an echo with a certain amplitude and structure. According to Grinnel[1] (ref. 14), some collicular neurons recover very quickly and sometimes show a supernormal phase in their recovery cycles. These neurons appear to be specialized for echo-detection.

EFFECT OF CONTRACTION OF MIDDLE EAR MUSCLES ON ECHO-DETECTION

For echo-detection, bats have not only the particular neural mechanism described above, but also a muscular mechanism. The middle ear muscles start to contract 4 to 10 msec earlier than sound emission and relax within 10 msec after the emission. The maximum contraction occurs at the moment of sound emission and reduces the stimulation of the bat's own ear as much as 20 dB (ref. 15). In cats, the middle ear muscles also contract preceding and during vocalization (ref. 16), but it is not as precisely timed as in bats.

The contraction of the middle ear muscles of bats actually improves detection, especially for echoes coming back from distances of more than 1 m. Figure 6A shows the re-

[1] Data by N. Suga and D. Crawley, unpublished.

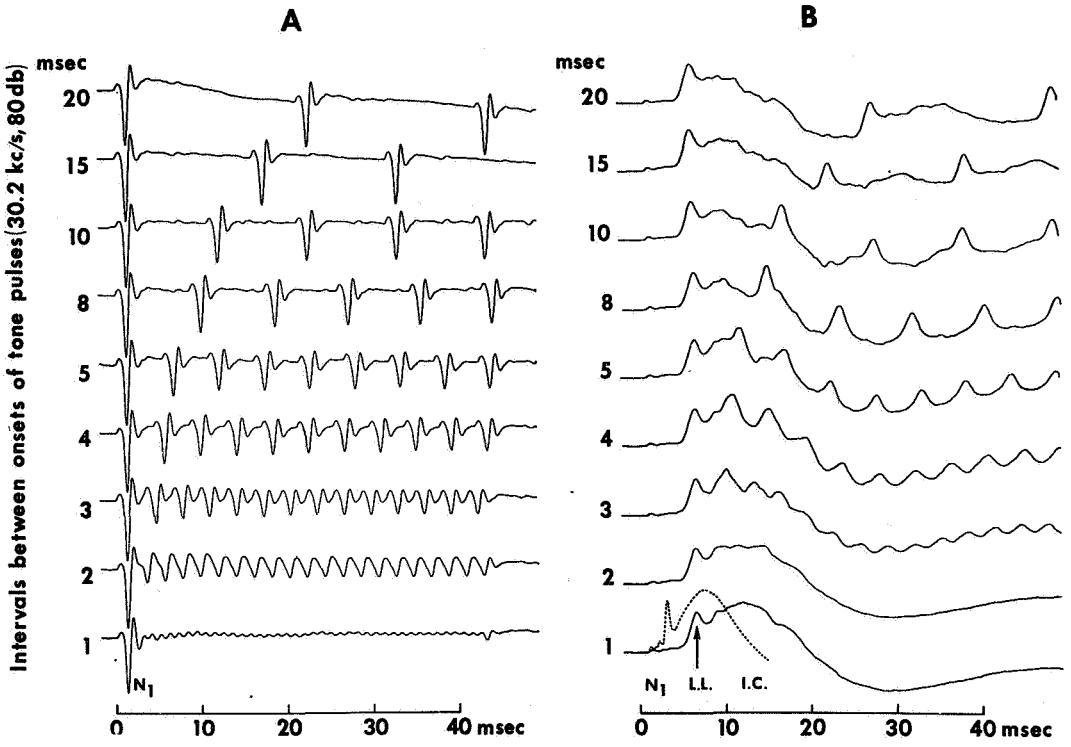


FIGURE 5. Responses to trains of 30.2 kHz, 80-dB SPL tone pulses, recorded from round window (A) and dorsal surface of inferior colliculus (B) of a 5-day old bat (*Myotis lucifugus*). Duration and rise time of each tone pulse were 0.5 msec and abrupt, respectively. Tone pulse was delivered intermittently during a 40-msec period which is indicated by time scale at bottom. Intervals between onsets of pulses is indicated to left of each trace. This train of pulses was delivered at a rate of two per sec. Responses to 64 trains were averaged with a computer, as shown in each trace. A—N_1 response. B—L.L. (arrow) and I.C. evoked potentials. N_1 follows repetitive stimuli at 1000 pulses per second. L.L. evoked potential fails to follow stimuli at about 400 pulses per sec. I.C. evoked potential does not follow stimuli at 80 to 90 pulses per sec. Note long latency of L.L. evoked potential. Shape of the I.C. evoked potential at the bottom of B is same as that evoked by 40-msec tone burst. Dotted curve shows L.L. and I.C. evoked potentials recorded from an adult bat (Suga and Crawley, unpublished data).

covery cycles of the I.C. evoked potential. When the first tone pulse is attenuated from 90 dB to 70 dB, for example, the recovery cycle of the response to the second tone pulse of 80 or 60 dB shortens. Since the evoked potential is a mass response, this shortening in recovery cycle may be considered to be the average change of many single neurons. The change in the recovery cycles of some collicular neurons is much more prominent than that in the recovery cycle of the I.C. evoked potential (fig. 6B and 6C).

INFERIOR COLLICULAR NEURONS SPECIALIZED FOR ECHO-RANGING

A basic clue for measurement of the distance to an object is given by the time lag

between the outgoing orientation sound and the returning echo. This time lag is presumably coded in the time difference between the responses of a neuron to the outgoing sound and the echo. Three questions must thus be asked:

(1) How is the zero time point reset?

(2) How is the arrival time accurately detected?

(3) How is the time lag measured?

The latency of response of a neuron to a stimulus generally changes as a function of stimulus amplitude and rise time. If the amplitude of a stimulus such as an outgoing sound is very large and quickly increases beyond the threshold of a neuron, the latency of response of the neuron will be short. If the amplitude of a stimulus such as an echo is just above the threshold of the neuron or if it slowly increases up to the threshold, the latency of response will be long. When this occurs, a large error will be introduced into distance measurement. Therefore, for echo-ranging there must be neurons that show relatively constant latency regardless of stimulus amplitude and rise time. If such neurons discharge multiple impulses in response to a single stimulus, there will be no way to distinguish between one strong echo and a few weak echoes. There must, therefore, be "*latency-constant neurons*" that do not fire repetitively for a single stimulus. Furthermore, the neurons must be spontaneously inactive. Any neurons satisfying the above requirements may be considered to be specialized for the measurement of distance and may be called "*echo-ranging neurons.*"

Unlike the cochlear nuclear neurons, most neurons in the inferior colliculus show no spontaneous discharges and fire only a few impulses at the onset of a sound stimulus (ref. 17). Most of the phasic on-responding neurons are not latency-constant units. The latency of response changes to a great extent

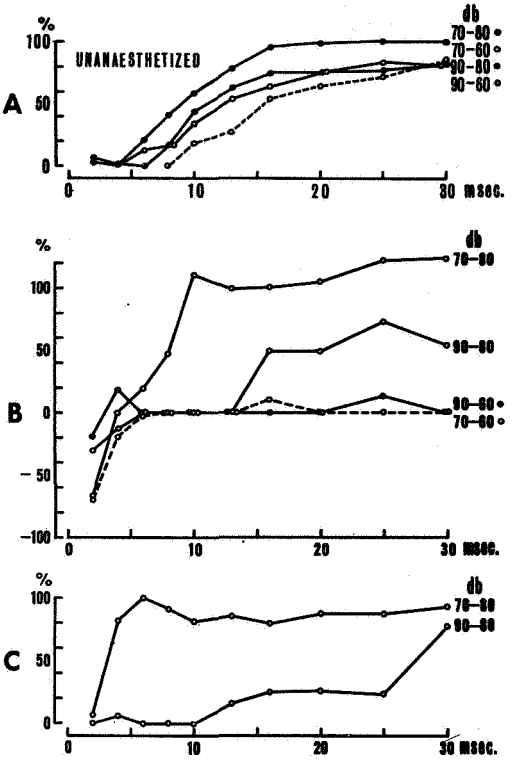


FIGURE 6. A—averaged recovery cycles of I.C. evoked potential obtained from five unanesthetized bats (*Myotis lucifugus*). B and C—recovery cycles of two inferior collicular neurons of anesthetized bats (*M. lucifugus*). Abscissas represent interval between onsets of a pair of FM tone pulses. Ordinates represent response to second tone pulse in percentage. Over 100 percent response signifies that the second pulse produced as large an evoked potential (A) or as many impulses (B and C) as when delivered alone; O means only the response to the first pulse, and negative values mean that even the response to the first pulse was reduced by percentage indicated. Amplitude of a pair of FM tone pulses is shown to the right of each curve (e.g., 70 to 80 means first tone pulse was 70-dB SPL, and the second, 80-dB SPL). Note changes in recovery cycle with change in relative amplitudes of tone pulses (ref. 12).

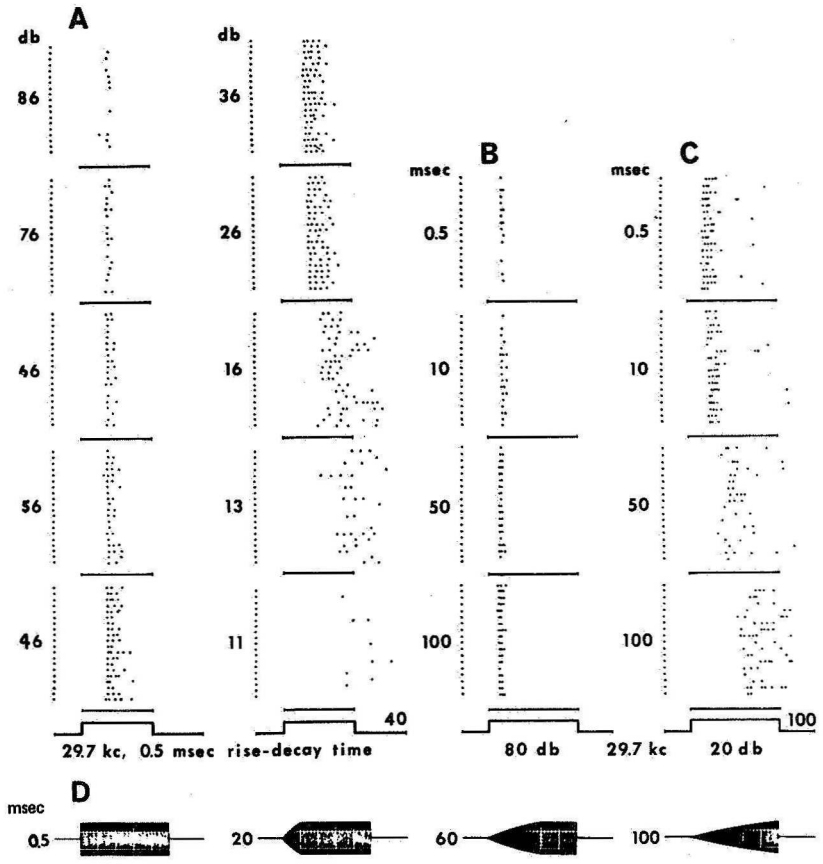


FIGURE 7. Responses of an inferior collicular neuron which was not specialized for echo-ranging (*Myotis lucifugus*). Responses to repeated presentations of same tone pulse are shown by a dotted pattern in which one dot corresponds to the peak of one action potential. Sweep of a cathode-ray oscilloscope was displaced vertically before each stimulus. Dots to the left mark the start of the sweep. Sound stimulus is represented by a horizontal bar and square wave at bottom of each dotted pattern. In A, the amplitude of a 29.7-kHz tone burst with a 0.5-msec rise-decay time and a 40-msec duration was attenuated from 86- to 11-dB SPL. In B and C, the rise time of a 29.7-kHz tone burst with a 100-msec duration was changed, as indicated by number to left of each dotted pattern. Decay time was always 0.5 msec. Peak amplitude of tone burst was 80-dB SPL in B and 20-dB SPL in C. Note changes in latency of response and number of impulses. In D, four samples of the 100-msec tone bursts used are shown (ref. 31).

with stimulus amplitude and rise time (fig. 7). Some of the phasic on-responding neurons, however, have the properties of the echo-ranging unit (ref. 31). For example, the neuron in figure 8 discharges one or less than one impluse per stimulus regardless of stimulus frequency, amplitude, and rise time. The latency of response stays almost the same regardless of stimulus amplitude. At 96 dB, the latency of the response to a tone burst with a 0.5-msec rise time was 5.7 $\pm$ 0.27 msec. Even if the amplitude was attenuated down to 56

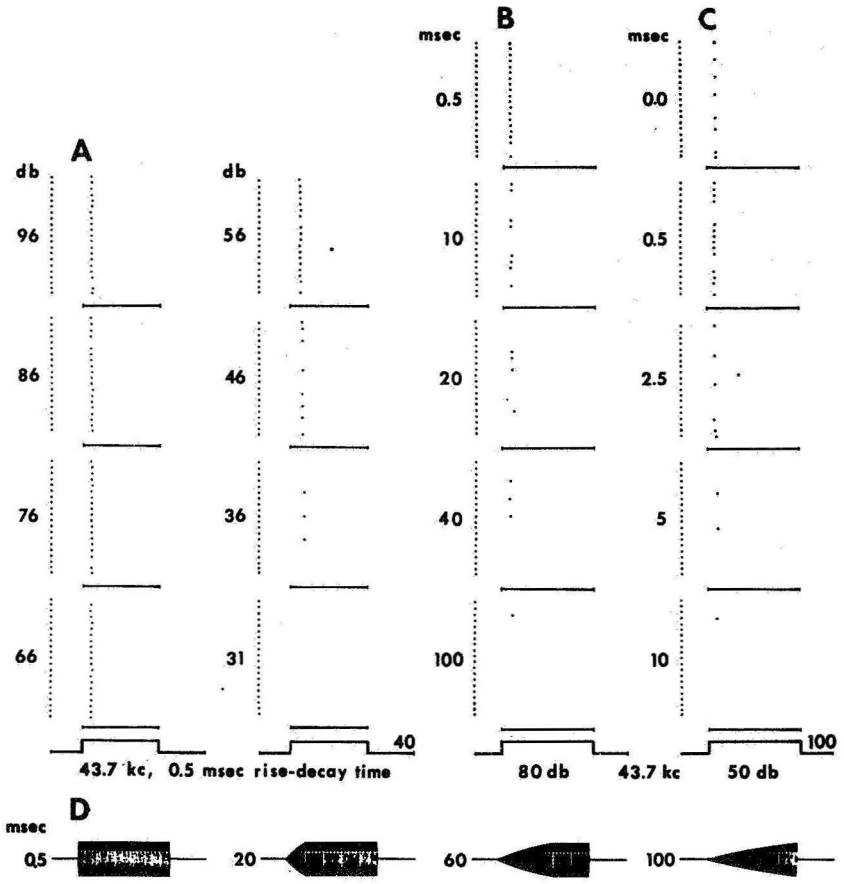


FIGURE 8. Responses of echo-ranging neuron in inferior colliculus (*Myotis lucifugus*). In A, the amplitude of 43.7-kHz tone burst with 0.5-msec rise-decay time and 40-msec duration is attenuated from 96- to 31-dB SPL. In B and C, rise time of a 43.7-kHz tone burst with 100-msec duration was changed, as indicated by number to left of each dotted pattern; decay time was always 0.5 msec. Peak amplitude of tone burst was 80-dB SPL in B and 50-dB SPL in C. Note that the number of impulses is always one or less than one, and the response latency does not fluctuate more than ±1.0 msec even if probability of response decreased down to 0.5. Symbols have the same meaning as in figure 7 (ref. 31).

dB (one one-hundredth), the latency was 6.2 ± 0.20 msec. Both the latency of response and the number of impulses per stimulus changed only a little, so the neuron can hardly code stimulus amplitude in this range. At the threshold amplitude the number of impulses per stimulus is very small. When an impulse does appear, however, its latency is nearly constant (fig. 8A). When the rise time of a tone burst increases from 0.5 to 98 msec, the number of impulses per stimulus becomes very small. When the response does appear, however, its latency stays within a very limited range (fig. 8B).

The minimum slope of the amplitude increase necessary for excitation of the neuron

is obtained by plotting the threshold of the response against the rise time (fig. 9). In figure 9, the threshold-rise time curves, a and b, make contact at 4 to 5 msec with the straight dashed lines which indicate the minimum slope. This means that the neuron can respond only to a tone burst with an amplitude which reaches the threshold within 4 to 5 msec, and that the "critical latency shift" due to the rise time is 4 to 5 msec. The smallest critical latency shift obtained was 1 msec. Since only a tone burst that quickly increases in amplitude can excite the neuron, the change in latency due to an increase in rise time is very limited in these neurons. The properties of these echo-ranging neurons can be explained by accommodation or a simple neural network model involving an inhibitory neuron.

We now know that the inferior colliculus receives impulses that are well synchronized with shortly spaced tone pulses, and that some of the inferior collicular neurons are specialized for the accurate detection of the onset of a stimulus. We should furthermore determine how the bat measures the time lag of an echo from the orientation sound. For the measurement of a time lag, the auditory system must include some kind of clock that is reset by each outgoing orientation sound. After being excited by the orientation sound, auditory neurons become insensitive for a certain period of time. The recovery cycle of response is more or less similar in all single units studied in the auditory nerve and cochlear nucleus (ref. 18). In the inferior colliculus, however, the duration of the recovery cycle varies considerably from neuron to neuron (fig. 10). Some neurons recover very rapidly, while others recover very slowly. This spectrum of recovery times may provide a mechanism for scaling the time lag of echoes returning from objects at different distances (ref. 12).

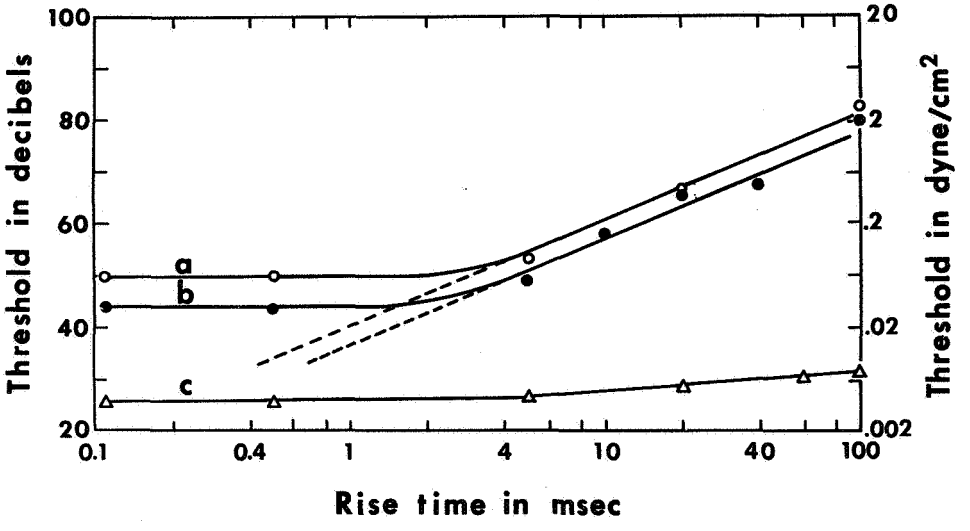


FIGURE 9. Change in threshold of response of three neurons (a, b, and c) with rise time of tone burst set at best frequency (*Myotis lucifugus*). Duration and decay time of the tone burst were 100 and 0.5 msec, respectively. Frequency of the tone burst was 70-kHz for a, 32-kHz for b, and 50-kHz for c. Dashed lines indicate minimum slopes of stimuli which excited neurons a and b (ref. 31).

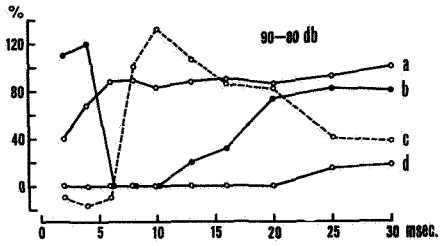


FIGURE 10. Four types of recovery cycles in the inferior colliculus (*Myotis lucifugus*). (a) short suppression, (b) delayed inhibition, (c) temporary recovery, and (d) undelayed inhibition. These were measured in four single neurons with a pair of 4-msec FM tone pulses, the first, 90-dB SPL and the second, 80-dB SPL. Ordinate represents response; abscissa, represents interval between onsets of first and second tone pulses in msec. A 100-percent response corresponds to number of impulses per second tone pulse when it was delivered alone. In these examples, this value was 1.00 for a, 2.75 for b, 1.28 for c, and 1.58 for d (ref. 12).

SOME NEUROPHYSIOLOGICAL DATA CONCERNING ECHO-LOCALIZATION

The structure of the superior olivary complex of bats, where binaural interaction first takes place, differs from that of cats (ref. 19). In cats, some of the neurons in a superior olivary complex are sensitive to very small interaural time and intensity differences (refs. 20 and 21). The properties of these neurons fit a neural model for sound localization (ref. 22). In the cat's inferior colliculus, there are neurons further specialized for processing information about sound localization. These neurons are very sensitive to either interaural time (or phase) or intensity differences (ref. 23). No comparable investigations have been performed on bats as yet.

The interaural intensity and phase differences due to the shadowing effect of the head and pinnae vary with stimulus frequency, so that the waveform of a complex sound at each ear is quite different from that of the original complex sound (refs. 24 and 25). The complex sound is more easily localized than is a pure tone. Pumphrey (ref. 26) explained how an animal could localize a sound source by listening to only a few short complex sounds delivered from it. His theory states that sound localization is accomplished by the binaural comparison of intensity ratios at three different frequencies to which the ears show different polar diagrams. To test this, measurements have been made of the polar diagrams of the ears of owls and bats, and it has been demonstrated that these polar diagrams change extensively with the frequency of sound and also with the position of the external ear (refs. 13, 27 and 28).

SOME NEUROPHYSIOLOGICAL DATA CONCERNING ECHO-ANALYSIS

Some insectivorous bats emit tone pulses that are variously modulated in amplitude and frequency. Echoes coming back from objects at different places overlap each other and show complex envelopes and structures differing from those of the outgoing sounds. In the inferior colliculus of these bats, there are neurons that are specialized for the analysis of a particular type of sound (refs. 29 and 30). One of the most interesting types of neurons is the FM-specialized neuron which responds to FM sounds but not to pure tones and noise bursts. For excitation of such a neuron, the direction, range, speed, and functional form of frequency sweep are important factors. Two factors which determine whether or not a complex sound will excite this type of neuron are the presence of a particular FM component within the sound and the components which exist simultaneously with the FM component. The nature of the sound preceding the complex sound is also an important factor.

Since most collicular neurons show phasic

on-responses to tone bursts, the rising phase of stimulus amplitude is very important for their excitation. Some neurons are sensitive to a fast rate of amplitude increase, while others are sensitive to a slow rate of increase. The shape and size of the tuning curves of some collicular neurons change greatly with the rise time of the sound used for the measurement (ref. 32). Some collicular neurons are specialized for responding only to sounds with a small amplitude (ref. 11). Some collicular neurons thus appear to have the capacity to analyze not only the frequency structure of echoes but also their amplitudes. In other words, these neurons can analyze echoes carrying information concerning such things as the size and surface properties of a target.

ACKNOWLEDGMENT

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DISCUSSION

QUESTION: Have you calculated sensitivity spectrums according to different frequencies?

SUGA: The frequency sensitivity of neurons differs from neuron to neuron. Some neurons are sensitive to 30 kc, while others are sensitive to 60 kc. There are a variety of neurons, each of which is tuned for a particular frequency of sound.

KLEEREKOPER: Do you assume that the mechanism you described serves as a timer?

SUGA: Yes, it is possible.

GRIFFIN: Have you compared the stability, the constancy of latency, with Dr. James Simmons' data on distance discrimination?

SUGA: The latency of response to a tone burst always shows some fluctuation, which introduces an error in echo-ranging. Responses of single neurons so far studied appear to be insufficient for explaining the fine distance discrimination demonstrated in the behavioral experiments because the standard deviation of a latency histogram is not very small. Further experiments on echo-ranging neurons and the statistical treatment of responses to artificial outgoing sounds and echoes should be performed. A neuron with interesting response properties was found in the inferior colliculus. That is, the latency of response to the second tone pulse showed a standard deviation much smaller than that of the latency of the response to the first one. There may be some neural mechanism by which the fluctuation in the latency of response is reduced.

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Middle Ear Muscle Contractions and Their Relation to pulse- and Echo-Evoked Potentials in the Bat (*Chilonycteris parnellii*)

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THE MUSTACHE BAT (*Chilonycteris parnellii*) emits orientation cries characterized by a long, 6- to 30-msec "pure tone" component and brief beginning and terminal FM sweeps (fig. 1). The long pulse durations make pulse-echo overlap inevitable under most conditions, and the question arises as to how the animals can effectively hear and analyze echoes that return during the emission of the intense outgoing pulse. In addition to the obvious masking problems during pulse-echo overlap, middle ear muscle contractions, if similar to those in other bats, should reduce hearing capacities during pulse emission and for several milliseconds thereafter (ref.1).

One method of recording the contraction characteristics of the middle ear muscles is to

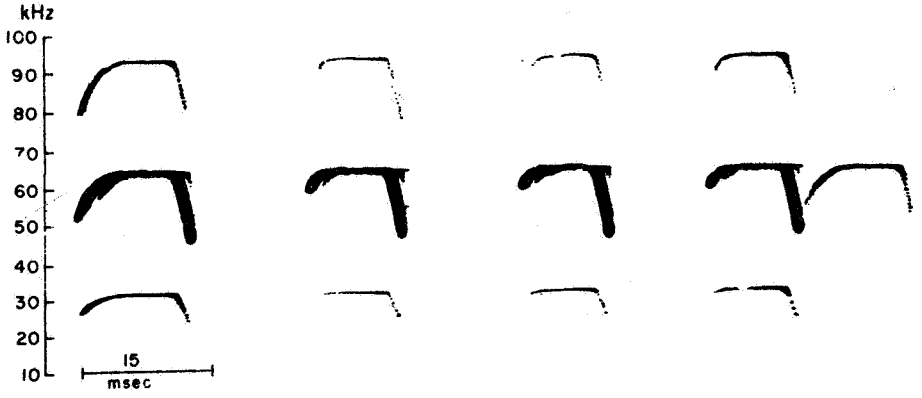

FIGURE 1. Sonograms showing frequency characteristics of pulses of *Chilonycteris parnellii parnellii*. Note strong 64-kHz second harmonic ("pure tone component") and the beginning and terminal FM components. Pulse number 1 on left shows unusually large initial FM component. Pulses 2, 3, and 4 are typical of those usually recorded from *Chilonycteris*.

place an animal in a pure tone, low frequency sound field and record the cochlear microphonic potentials evoked by the sound field. By observing the attenuation of the microphonic potentials, it is possible to record the exact time at which the muscles begin to contract, the speed of the contraction, the degree of contraction, and the time and rate of relaxation. This is the method which was successfully used in establishing the functional role of the muscles in the Mexican free-tailed bat (*Tadarida*) (refs. 1 and 2).

Recent application of this technique to *Chilonycteris* has yielded results which differ from those reported for *Tadarida* but which correlate with previous work dealing with pulse- and echo-evoked potentials in active *Chilonycteris*. In this report attention will be directed to:

(1) Characteristics of pulse- and echo-evoked potentials under various conditions

(2) Evidence of changes in hearing sensitivity during and after pulse emission

(3) The role of the middle ear muscles in bringing about these changes

MATERIALS AND METHODS

The bats used in this study were *Chilonycteris parnellii parnellii* (Gray) of the family Phyllostomatidae. The animals were captured in Jamaica and maintained in captivity on a diet of mealworms.

For recording cochlear microphonic potentials small stainless steel wires with the tips melted into a ball were chronically implanted on the round window of the cochlea. Uninsulated stainless steel insect pins (#00) placed within the substance of the inferior colliculi were used for recording evoked neural potentials. The techniques for recording cochlear potentials and brain potentials from unanesthetized, flying bats have been described previously (refs. 1 and 2).

Pulse- and echo-evoked potentials were studied under three different experimental conditions—in a small box; in a large chamber; and when flying within the chamber. The dimensions of the small box ($30 \times 30 \times 30$ cm) were such that the bat was always within 15 cm of one wall and most of the loud echoes should have returned to the bat's ear within several milliseconds. The large recording chamber measured approximately $3 \times 3 \times 3$ m and echo delays up to 17 msec were possible. The chamber was completely lined with orlon pile to reduce reverberating echoes; the floor of the chamber was covered with a carpet. The rug, the recording equipment, and the landing area probably produced the loudest echoes.

The exact position of the bat in the box or in the recording chamber at a given instant was not determined, but approximate positions were recorded by voice on one channel of a tape recorder (Precision Instrument Co., Model Pi–6100). The physiological potentials and the pulses emitted by the bats were recorded on other channels of the tape recorder.

Records of pulse- and echo-evoked neural potentials were obtained from seven animals; however, in only three of the seven did the animals appear to regain their preoperative state of health, as judged by strong flight and obstacle avoidance skills. The most extensive records were obtained from two animals with electrodes implanted in both inferior colliculi; potentials were recorded over periods of 6 and 9 days. In most cases the experiments were terminated when the electrode assembly became dislodged from the animal's head.

Chilonycteris did not tolerate extensive surgical exposure of the skull and round window; anchoring electrodes to only small exposed areas of the skull did not provide permanent preparations. Almost all of the cochlear microphonic potentials examined were

from two animals from which potentials were recorded for periods of 2 and 3 days after implantation of the electrodes. Although there was clear evidence of middle ear muscle contractions in all of the preparations, the amount of attenuation of the cochlear microphonic potentials was usually small in comparison with that observed in the Mexican free-tailed bat (*Tadarida*). The smaller attenuations (weaker contractions) in *Chilonycteris* may be attributed to the short postoperative recovery time and/or to differences in the development of the muscles. In *Tadarida*, which have very large muscles (ref. 3), strong muscle contractions were often not observed until 5 to 7 days after the operation (ref. 1), and the maximum amount of attenuation of the cochlear potentials ranged between 25 and 30 dB for the frequencies included in the emitted pulses. This amount of attenuation is sufficient to reduce an evoked potential of near maximum amplitude to a nondetectable response. In *Chilonycteris* even a 10 dB attenuation of the echo energy could account for the results observed in this study.

RESULTS

Pulse and Echo-Evoked Potentials

In all recording situations and in almost all records it was possible to identify three distinct fast wave potentials evoked by different components of the emitted pulse. These were most easily identified in the small box or in other confined spaces where there were no large echo-evoked potentials superimposed on the pulse-evoked potentials (fig. 2). The first fast wave potential was clearly associated with the beginning of each pulse. Its latency was on the order of 3.0 to 3.5 msec, and it represents the N_4 "on" response (ref. 4). Studies on *Myotis* have shown that this fast wave represents the lemniscal input

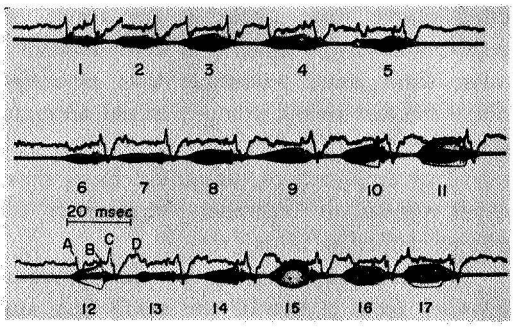

FIGURE 2. Typical examples of pulse-evoked potentials elicited by a bat's cry. Each upper trace shows evoked potential recorded from inferior colliculus; lower trace of each pair shows emitted pulse as detected by microphone placed several inches from the bat. Records were taken while the bat was in a small confined space so that echoes were reflected directly back into the ears. A—N_4 "on" response to the pulse's beginning, B—N_1 response probably to termination of the pure tone component or beginning of terminal FM sweep; C—sharp positive peak typical of "terminal" N_4 response; D—slow wave potential.

to the inferior colliculus (ref. 5). The second fast wave potential occurred within 1.0 msec of the termination of the pure tone component of the emitted pulse, or conversely, within 1.0 msec of the beginning of the terminal FM sweep. The amplitude of this potential was always small, and its latency was short; these characteristics suggest that it represents the N_1 (auditory nerve) potential. It is curious, however, that this potential was seldom seen in relation to the beginning of a pulse or in relation to echo-evoked potentials even when the echo-evoked N_4 potentials were large. The most consistent of all of the fast wave potentials was the "terminal" N_4 potential. This occurred 3 to 4 msec after the end of the pure tone component. The positive peak of the terminal N_4 response was not always sharp and distinct, but the negative going slope was always steep and easily recognizable. The fast wave peaks

noted above were probably the result of synchronous neural activity in many auditory units; slow wave potentials that typically follow the fast waves in anesthetized animals were seen (fig. 2), but they were often obscured by echo-evoked potentials. Such slow waves appear to represent the activity of inferior collicular units (ref. 5).

Typical examples of the evoked responses recorded from a bat in the small box are shown in figure 2. In these records the variable nature of the N_4 pulse "on" response is evident. The "on" responses are particularly large in relation to pulses 1, 3, and 4, but they are small and indistinct in relation to pulses 8, 9, 10, and 11. At fast pulse repetition rates the "on" response was often most pronounced in relation to the first pulse in a series, but no clear correlation could be found between the amplitude of the "on" response and the interpulse interval. Thus small "on" responses could not be correlated with poor recovery due to small interpulse intervals. In addition, no relationship could be found between the rise time of the emitted pulse and the amplitude of the "on" response. (For example, compare the rise times and the evoked responses shown in relation to pulses 9, 10, 11, and 12 in figure 2.) The amount of FM sweep showed no correlation with the amplitude of the pulse-evoked "on" response; large sweeps, similar to those shown for pulse 1 (fig. 1), sometimes produced smaller responses than did pulses showing little or no FM sweep.

The rise time and the amount of FM sweep at the beginning of a pulse are variable, especially when compared to the fall time and the amount of the terminal FM sweep. The more constant physical features at the end of the pulse are probably related to the consistent shape and amplitude of the pulse-evoked terminal N_4 potential. In almost all records there was a striking similarity in the pulse-evoked potentials from one pulse to the next. This is clearly evident in figures 2 and 3.

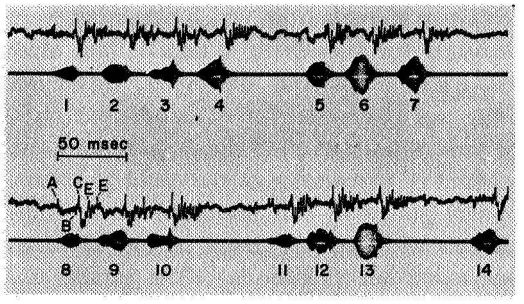

FIGURE 3. Pulse- and echo-evoked potentials recorded from inferior colliculus of *Chilonycteris*. Bat was on the ceiling of large recording chamber. A—N_4 "on" responses; B—N_1 response to "terminal" component of pulse; C—N_4 response to terminal component of pulse; E—echo-evoked potentials. Lower trace of each pair shows emitted pulses; pulses 1 to 7 are shown in upper record, and pulses 8 to 14 are shown in lower record.

The responses shown in figure 3 were recorded from a bat hanging on the wall of the large flight chamber. In relation to every pulse there is a distinct N_4 "on" response and an even more prominent N_4 terminal response; following the terminal N_4 pulse-evoked potential, there is a whole series of echo-evoked potentials. Although the exact origin of the echoes could not be established, there were a number of factors indicating that they were in fact echo-evoked potentials. First, such potentials were never recorded in the closed-space situations where all the echoes should have returned to the ear within a few milliseconds. Second, when the potentials did occur, their time of appearance after the pulse-evoked potential was consistent with the calculated echo delays for each situation. The most convincing evidence (ref. 2), however, is from the conclusive demonstration that the intervals between pulse- and echo-

evoked potentials continuously shortened in flying bats as they approached a known target (fig. 4).

There are three particularly important features shown in figure 3:

(1) All distinct echo-evoked potentials appear after pulse emission, and they occupy the intervals between pulses.

(2) There is a distinct neural silence between the N_4 "on" response and terminal N_4 response.

(3) The number of echo-evoked potentials is dependent on the interpulse interval. For example, there are four or five echo-evoked potentials which occur in the 8 msec interpulse interval between the end of pulse 11 and the beginning of pulse 12 (the fifth potential may be an "on" response to pulse 13). In the 12 msec interval between pulses 12 and 13 there are seven or eight echo-evoked potentials. After pulse 13, the last in the series, there are nine echo-evoked potentials. A large number of records similar to those shown in figure 3 have been analyzed. In almost all cases there were no echo-evoked "on" responses, and no distinct echo-evoked potentials of any kind could be identified consistently during pulse emission. After each pulse there was always a number of echo-evoked potentials. The only cases where echo-evoked potentials to a first pulse were recorded while a subsequent pulse was being emitted was when the second pulse was very faint.

Records obtained from flying bats were particularly interesting with respect to the amplitude of the echo-evoked potentials compared to pulse-evoked potentials. The echo-evoked potentials were as high as, or in many cases much higher in amplitude than, the pulse-evoked potentials (figs. 4 and 5). If the amplitude of the evoked potential reflects the number of units responding synchronously, it seems that the echoes are exciting more units

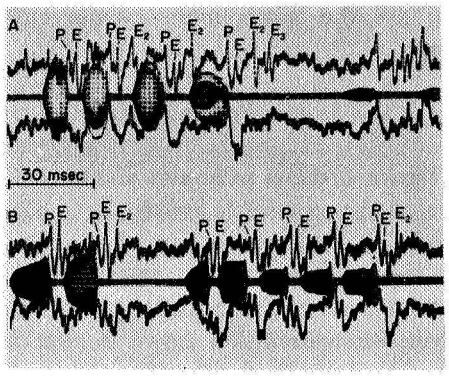

FIGURE 4. Neurophysiological evidence of focusing. Middle trace of each record shows emitted pulses; upper trace shows evoked potentials recorded from right colliculus; lower trace shows left collicular records. Echo-evoked potentials (E) recorded from right colliculus are masked if echoes return while subsequent pulse is being emitted. In A, echo-evoked response E_2 is large and distinct after pulses 2, 3, and 4 where it occurs during the interpulse interval. E_3 occurs only after pulse 4 where the interpulse interval is long. In B, echo-evoked potential E_2 is large and distinct after pulses 2 and 7. There is no distinct "E_2" potential following pulses 1, 3, and 6 where the interpulse intervals are short. In relation to pulses 4 and 5, there is a potential when the E_2 response should occur; these, however, also correspond to the appearance of the "on" responses for pulses 5 and 6.

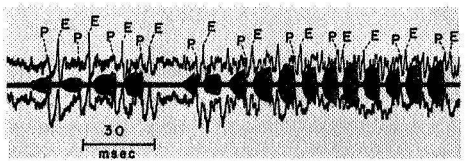

FIGURE 5. Pulse- and echo-evoked potentials recorded from right (upper trace) and left (lower trace) inferior colliculi of flying *Chilonycteris*. Middle trace shows pulses as detected by a microphone. Note the very high amplitude of the echo-evoked potentials (*E*) recorded from the right colliculus. As bat approaches target (a landing area), echo-evoked potentials occur closer to the pulse-evoked potentials (*P*), and their amplitude diminishes.

than are the much more intense emitted pulses.

The Middle Ear Muscles

Figure 6 shows examples of the cochlear microphonic potentials evoked by a 12-kHz sound field and attenuation of these potentials by contractions of the middle ear muscles. The most consistent type of microphonic attenuations are shown in relation to pulses 1, 5, 7, 8, 9, 11, 20, and 21. The muscles began to contract almost simultaneously with the beginning of each pulse, reached a maximum state of contraction prior to the terminal FM sweep, relaxed over the duration of the FM sweep, and completed the relaxation phase within 2 or 3 msec after the termination of the pulse. The attenuation shown in relation to pulse 3 is one of the strongest recorded, and in this case the contractions started about 4 msec prior to pulse emission. When faint pulses were emitted (e.g., pulses 4, 6, 10, 12, 13, 24, and 25), there was little or no evidence that the middle ear muscles contracted. During the terminal phase of echolocation or in other situations where *Chilonycteris* emitted pulses at very fast repetition rates (pulses 14 to 19, fig. 6), the muscles appeared to remain tonically contracted while the entire series of pulses was emitted.

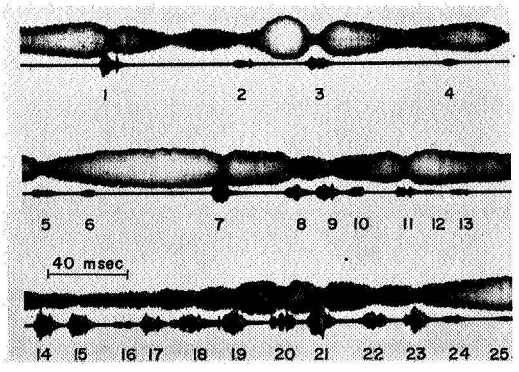

FIGURE 6. Middle ear muscle contractions in relation to pulse emission. Upper trace of each record shows 12-kHz sound field-evoked cochlear microphonic potentials, and lower trace shows emitted pulses detected by a microphone.

DISCUSSION

There appears to be one specific part of the bat's cry and of each returning echo that causes the synchronous firing of many auditory units and gives rise to the sharp, very distinct "terminal" N_4 potential. It was originally thought that this potential was evoked by the beginning of the FM sweep and thus represented an "on" response (ref. 2). Grinnell (ref. 6), however, has pointed out that it could be evoked by the termination of the pure tone component of the pulse. Both of these events occur simultaneously. Another possibility is that many units are excited at the instant the FM component sweeps through a specific frequency to which the ear is sharply tuned (ref. 7).[1] In *Chilonycteris* it has been shown that hearing is very sharply tuned over a narrow 1- or 2-kHz band which corresponds in frequency to the second harmonic of the emitted pulse (ref. 6).

Regardless of the origin of the potential, it can be demonstrated that there is a linear relationship between stimulus intensity and the amplitude of the evoked potentials at low and moderate sound pressure levels (ref. 2). At high sound pressures the linearity does not always exist, and a very loud pulse may produce a smaller response than a fainter pulse. Thus it is not correct to conclude that changes in the amplitude of the N_4 potential represent changes in sensitivity when dealing

[1] HENSON, O. W., JR.: The Ear and Audition. *In*: Biology of Bats. Vol. II. W. A. Wimsatt, ed., Academic Press (in press).

with loud signals. In the present study sensitivity changes were assessed on the basis of the presence or absence of echo-evoked potentials and not simply on minor amplitude changes. Under the "open space" experimental conditions, it seems unlikely that any of the echoes were extremely loud. In interpreting the results, it has been assumed that the fast wave N_4 potential indicates a synchronous firing of many units and that the appearance of the fast wave potential in relation to the echo is an important part of the echo detection system. Failure to record a potential not only indicates a lack of, or marked decrease in, synchronous firing, but it also suggests a reduction in sensitivity. The proposed reduction in sensitivity should not be equated with a lack of perception.

There are several findings in the evoked potential records which clearly indicate a decrease in sensitivity during pulse emission. "On" response echo-evoked potentials were seldom observed, and under the experimental conditions the beginning of the echoes should have returned while the pulse was being emitted. Also, there was usually little or no evidence of any type of potential while the pulse pure tone was being emitted (figs. 2 and 3). Most convincing was the finding that a specific "terminal" N_4 echo-evoked potential was large if it returned during the interpulse interval but would disappear if the echo returned while the next pulse was being emitted. Many records were obtained in which an echo-evoked potential would appear, disappear, and re-appear depending on whether or not the echo was overlapping the pulse (figs. 3 and 5).

It is important to note that the sensitivity changes indicated by the evoked potentials are exactly what one would expect knowing the contracting characteristics of the middle ear muscles. If muscle contractions start before or simultaneously with the beginning of the emitted pulse and reach a maximum state of contraction prior to the terminal FM sweep, then the energy at the beginning of an echo should be less efficiently transferred to the cochlear fluids than the energy at the beginning of the pulse. On the other hand, since middle ear muscle relaxations begin about the time of the terminal FM sweep and are completed within a few milliseconds after the end of the pulse, the FM echo energy should be transferred more efficiently than the FM pulse energy. This is at least a partial explanation for the very large echo-evoked potentials seen in flying bats.

It is important to note that under all conditions the first high amplitude echo-evoked potential to occur after each pulse was seen only when the pulse-echo delay was more than 3 msec; also important is the fact that the echo-evoked potentials became smaller in amplitude as the pulse-echo delay decreased (fig. 4). These observations can be correlated with the degree of muscle relaxation at specific points in time after the beginning of the terminal FM sweep.

The crucial experiment of denervating or ablating the middle ear muscles and then examining the evoked potentials has not been accomplished; it seems unlikely that the animals would survive such an extensive surgical procedure or that they would continue to emit intense pulses after such an operation. As noted above, however, our records indicate that the middle ear muscles do not contract when faint pulses are emitted (fig. 6), and in this connection it should be recalled that distinct echo-evoked potentials were recorded during pulse emission only when the second pulse was much fainter than the first.

In anesthetized *Chilonycteris* the N_4 sensitivity to the second of two identical signals is progressively reduced as the interstimulus interval is decreased (ref. 2). This may contribute to the small amplitude of the echo-

evoked potentials immediately following a pulse, but there are several points which suggest that the muscle contractions are more important in bringing about the amplitude reduction than are the recovery periods. Middle ear muscle relaxation during the terminal FM sweep in *Chilonycteris* is similar to middle ear muscle relaxation in *Tadarida*, and it has been observed that the cochlear microphonic potentials evoked by echoes in flying *Tadarida* become progressively smaller in amplitude as the animal approaches an echo source (ref. 2). Since the cochlear microphonic potential does not have a recovery period, the changes in amplitude can be attributed to incomplete relaxation of the middle ear muscles.

A second factor suggesting that middle ear muscle contractions are more significant than recovery periods in producing the results is that high amplitude evoked potentials were often recorded from *Chilonycteris* when the interval between the two echo-evoked potentials was only 1 or 2 msec (fig. 3). Although the relative intensities of the different echoes are not known, the responsiveness of the system to successive sounds appears to be considerably greater than has been observed in anesthetized preparations. In anesthetized *Chilonycteris* the time required for the evoked responses to show a 100-percent recovery for short trains of 90-dB (re-0.0002 dyne/cm^2) pulses was usually more than 10 msec, and in most cases no responses were observed when the interstimulus interval was less than 3 or 4 msec (ref. 2). Thus the system seems considerably more responsive to successive sounds in the unanesthetized than in the anesthetized animal at times when the middle ear muscles are relaxed.

There are a number of factors other than middle ear muscle tension that can control auditory input to some degree; these include ear position (refs. 2 and 8 to 11), auditory canal closure (ref. 11), and auditory feed-back systems within the CNS (ref. 12). By using relatively low frequencies for the pure tone sound field, the effect of the external ears and ear closure was minimized. From direct observation of these structures in *Chilonycteris* it is our opinion that they were not operating in such a way as to attenuate the sound field-evoked microphonic potentials in the brief time before, during, and after pulse emission. Furthermore, in both the round window implants and the inferior collicular implants, the mobility of the external ears was greatly reduced by the surgical procedure required to expose these structures; in all cases the extrensic ear muscles had to be severed from their origins on the back and top of the skull.

The possibility that efferent systems and/or pulse-echo interaction in the form of masking are contributing to the results of this study cannot be discounted. However, such factors, if present, appear to be operating at the same time and in much the same way as the middle ear muscles. In any case, sensitivity to echoes is at its best in the interval between pulses. In the past, the author has advocated that bats may be able to control the "echolocative depth of field" by controlling the duration of the interpulse interval (refs. 1 and 2). This idea was based on the known activity of the middle ear muscles in *Tadarida* and on the echo-evoked potentials in *Chilonycteris*. With the available data on evoked potentials and middle ear muscle activity for the same species, the assumption seems even more plausible than before.

SUMMARY

The orientation cries of the bat (*Chilonycteris parnellii*) are characterized by

three distinct components — a beginning FM sweep, a long pure tone, and a terminal FM sweep. A bat's own cry evokes two consistent fast wave (N_4) potentials; the first is a response to the beginning of the FM sweep, and the second "terminal" N_4 potential is evoked by the off of the pure tone component and/or by some part of the terminal FM sweep. The "terminal" N_4 potentials were the only type consistently recorded in response to echoes. Echoes overlapping the outgoing pulse or a subsequent pulse did not produce distinct responses, but those returning during an interpulse interval produced high amplitude potentials. These results are consistent with the hypothesis that the bats can control the "echolocative depth of field" by regulating the interpulse interval. Echoes appear to be processed much more efficiently than the outgoing pulses, and this can be readily accounted for by the action of the middle ear muscles. In flying bats the echo-evoked potentials were much higher in amplitude than pulse-evoked potentials.

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Individual Recognition Between Mother and Infant Bats (*Myotis*)

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INDIVIDUAL RECOGNITION AMONG BIRDS has received a great deal of attention (refs. 1 to 6), while among mammals the literature on this subject is relatively sparse. Marler (ref. 7) noted individual differences in a typical call pattern of wild chimpanzees. Bartholomew (ref. 8) described individual recognition between mother and infant Alaskan fur seals. Bowers and Alexander (ref. 9) demonstrated that olfactory cues were used by laboratory mice to discriminate between individuals. Human mothers can identify their own infant's hunger cry from those of other infants (ref. 10).

Individual recognition is ultimately based on some form of communication; visual, olfactory, auditory, tactile and/or gustatory stimuli provide the cues for identification. Animals tend to emphasize one avenue of communication more than others, and the kinds of stimuli utilized depend on the habitat and mode of life of the species (ref. 11). Thus with the nocturnal bats, one might expect auditory and/or olfactory stimuli to take precedence over visual cues. In the few genera of bats that have been studied, the mother selectively nurses only her own young, i.e., *Eptesicus* (ref. 22), *Pteropus* (ref. 13), *Nycticeius* (ref. 14), and *Tadarida* (ref. 15). Selective nursing implies individual recognition. Mohres (ref. 16) and Kulzer (ref. 15) have suggested that bat ultrasonics may function in communicating as well as sensing. Several authors have described the continuous nature of calls emitted by infant bats and concluded that they serve to attract the mother to the infant (refs. 12, 14, 15, 17, and 18). Novick (ref. 19) has suggested that the diverse echolocation sounds in different species of bats may be correlates of different sonar systems. But these differences in duration, intensity, and frequency could also contribute to the uniqueness of the sounds as communicative signals. Marler and Hamilton (ref. 20) and Mohres (ref. 16) suggest that the pulse characteristics could serve as a cue for localization by the mother. Individual recognition based on auditory stimuli could prove very useful to the bat. When the mother returns to the nursery colony after her daily feeding excursion, she must locate her own infant. The colony is increasing in

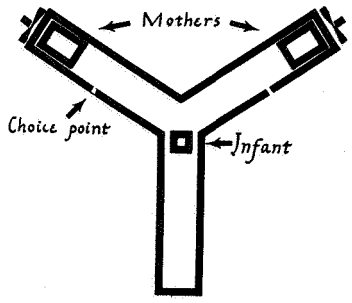

FIGURE 1. Diagram of Y maze apparatus.

numbers daily, and her infant becomes more mobile with maturation. There is evidence[1] that the infant's voice characteristics change as it grows, and this may provide the individuality necessary for recognition. This remains to be seen. In this paper, the authors have attempted to determine whether individual recognition occurs in the little brown bat (*Myotis lucifugus*), and if so, what the basis for that recognition is.

METHODS

Mother-infant pairs of *Myotis lucifugus* were captured from Baltimore nursery colonies and brought into the laboratory in June 1970. When captured, infants ranged from 1 to approximately 4 days old. Cornell mosquito cages, 30½ cm³, contained the bats in a room held at 32° C. with circulating air. Humidity was maintained by placing several large evaporation trays on the floor. The bats were fed and watered once a day but otherwise disturbed as little as possible. Bats were identified by bands and toe clips. For other details on care and feeding, see Gould.[1]

The experiments were conducted in a second room, kept at the same temperature and removed from the animal room by still a third room. An aluminum sided Y maze was used to test the ability of the infant to recognize its mother on the basis of auditory communication (fig. 1). Each arm of the maze measured 65 × 14 × 17 cm. The top of each arm was covered by a sliding plexiglass sheet. Guarded fans (10 cm diam), which moved 50 cfm/fan, were placed on two arms of the Y to draw air out of the chamber. The maze was positioned so that varying conditions in the room, such as overhead lights, would be accounted for.

Two mothers were separated from their infants and each one randomly placed in a holding box, 17 × 10 × 12.5 cm, at the end of an arm. These cardboard holding boxes had double screening on the end facing the junction of the maze; fine screen was used to eliminate the use of vision by the infant. The opposite end of the box had a single layer to allow the air to be drawn out of the chamber. The infant to be tested was placed under a ¼-in. hardware cloth cover at the junction of the arms where its mother and an alien mother were located. The alien mother's infant was removed to the animal room. After a 10-min waiting period, the cover on the test animal was gently lifted and the infant's movement recorded. This waiting period was designed to allow ample time for the infant to calm down and for communication between the bats to occur. A point 35 cm down each arm was arbitrarily taken to be the "choice" point, although in every case, the infant went all the way to a box holding an adult.

Between each run, papers were laid down to minimize the possible effect of a scent trail. Several infants were used more than once, but only after a minimum 72-hr interval between runs. In all cases, the adults were randomly placed at the maze arms. However, it should be noted that when the alien moth-

[1] GOULD, E.: Studies of Maternal–Infant Communication and Development of Vocalizations in the Bats *Myotis* and *Eptesicus*. Commun. Behav. Biol. (in press).

er's infant was tested, the random placing of the two mothers was sometimes such that their positions remained the same as when the first infant was tested.

Twenty runs were completed in this manner using 13 mother-infant pairs. The last nine runs were recorded at 30 ips using a Precision Instrument Tape Recorder No. 202, modified Granath ultrasonic microphone system, to test whether the bats were emitting ultrasonic communication signals. The recorder was turned on after the adults were in position and just before the door was opened to permit entry with the infant to be tested. Later, the recordings were slowed 16 times, played through a Tektronix Type 503 Oscilloscope, and filmed with a 35 mm Kymograph Camera Model C4–K. The communication signals were first described by Gould,[2] who listened to the slowed sounds of isolated infants and isolated adult mothers. He was able to distinguish the mother and infant when they called simultaneously on the same tape, and his description of the vocalizations was used in this experiment. The total number of antiphonal chirps from each mother was tabulated. Isolation call-antiphonal chirp pairs were randomly selected from the tapes and filmed for duration analysis. A standardized technique was used to measure the length of the *i* call, and then the span from the end of the *i* call to the beginning of the *A* chirp. The interval from the beginning of the *i* call to the beginning of the *A* chirp was also measured.

RESULTS AND DISCUSSION

It can be seen from table 1 that infants chose their own mothers in 15 of the runs and the alien mothers five times. Isolation calls were emitted by infants during all of the nine recorded runs, but mothers answered these vocalizations with antiphonal chirps in only eight runs. One notes from table 2 that ultrasonic communication occurred during several runs in which the infant made an incorrect choice. Also, there were no antiphonal chirps emitted during run number 15, an incorrect choice.

TABLE 1.—*Results of the Y Maze Test*

Date	Infant number	Mother number	Alien mother	Choice
21 June	a	1	6	Mother
22	b	2	3	Mother
22	c	3	2	Mother
24	d	4	5	Mother
24	e	5	4	Mother
25	f	6	1	Mother
25	a	1	6	Mother
25	g	7	14	Alien
26	h	8	9	Mother
29	f	6	4	Mother
29	d	4	6	Mother
30	e	5	2	Alien
1 July	i	9	10	Mother
1	j	10	9	Mother
1	a	1	2	Alien
1	b	2	1	Alien
2	k	11	7	Mother
2	g	7	11	Mother
2	l	12	15	Alien
6	m	13	9	Mother

From this experiment, the authors have concluded that individual recognition between mother and infant did occur. However, it cannot be determined at this time if the recognition was based on ultrasonic communication or olfactory stimuli. The infant was prohibited from receiving odors of either adult, yet it is possible that the mother recognized the odor of her infant in the air being drawn past her. She may have then called in response to the olfactory stimuli and/or the

[2] GOULD, E.: Studies of Maternal-Infant Communication and Development of Vocalizations in the Bats *Myotis* and *Eptesicus*. Commun. Behav. Biol. (in press).

TABLE 2.—*Analysis of Recorded Runs*

Run number	Approximate age (days)	*i* calls	*A* chirps	Number *A* chirps	Choice
12[a]	23	yes	yes	96	2×Mother 1×Alien
13	13	yes	yes	388	Mother
14	7	yes	yes	106	Mother
15	12	yes	no	none	Alien
16	17	yes	yes	7	Alien
17	9	yes	yes	8	Mother
18	23	yes	yes	7	Mother
19	5	yes	yes	115	Alien
20	15	yes	yes	654	Mother

[a] Twice during this run, the infant pushed the hardware cloth cover toward the mother's arm of the maze. When released after 10 min., the infant chose the alien mother.

infant's isolation calls; and the infant, in turn, chose the only arm of the Y maze carrying auditory stimuli. However, it is significant that the infant responded to the mother's vocalizations. As for the five incorrect choices, it is possible that the system is only 75-percent efficient. At this time, we are unable to determine whether one or both adult mothers responded to the infant calls. Several of the incorrect choices were made in unrecorded runs and may or may not have involved antiphonal calling by the mother.

If the basis for recognition is ultrasonic vocalization, one must assume that there is sufficient variability in individual calls and that this variability is utilized by the bat. Bateson (ref. 21) in discussing dolphin vocalization suggests that we will not know much about the communication process until we know what one dolphin reads in another dolphin's signals. The same holds for bat communication. The literature on the individuality of bat vocalizations is sparse, but the authors have found statistical differences (99-percent level of significance, parametric analysis of variance) between the different mother-infant pairs in the duration of an infant's *i* call, the interval from the end of the *i* call to the beginning of the *A* chirp, and the interval from the beginning of the *i* call to the beginning of the *A* chirp.

Overlaps occur between *i* call durations of different infants (fig. 2) and between intervals of different mother-infant pairs (figs. 3 and 4). One might argue that because of these overlaps, *i* call duration would be a poor substrate for individual recognition. However, in a large nursery colony, any clue might help the mother locate her infant. Perhaps at least a portion of the population could be eliminated by hearing *i* calls of vastly different duration than those of her own infant. Final recognition may be based on olfactory cues as in *Rousettus* (ref. 22). There appears to be no apparent relation between the *i* call duration and the age of the infant. Nor can any conclusions be drawn concerning the numbers of antiphonal chirps required for the infant to localize the mother. Since differences between mother-infant pairs

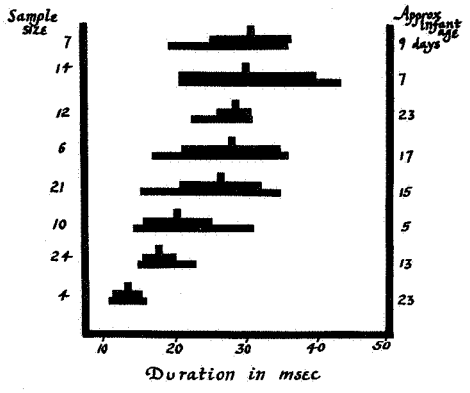

FIGURE 2. Duration of isolation call. Lower bar of each triplet shows range data for each infant. Center bar shows ±1 standard deviation from the mean. Upper bar represents mean duration of that infant's call.

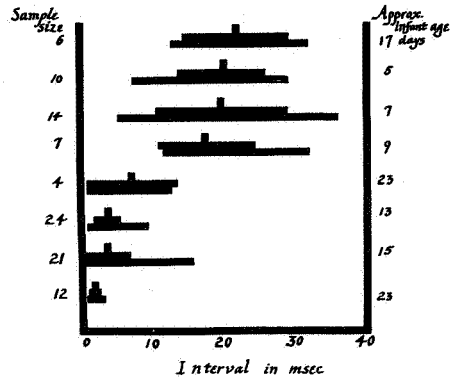

FIGURE 3. Interval from end of isolation call to beginning of antiphonal chirp. Lower bar of each triplet shows range of intervals for each mother-infant pair. Center bar shows ±1 standard deviation from the mean. Upper bar represents mean of the intervals.

in the interval from the end of an *i* call to beginning of the *A* chirp exist, it is possible that the infant may utilize this information and crawl toward the mother or modify its vocalizing pattern. Therefore, at least two possible variables in the vocalizing behavior of *Myotis* exist: *i* call duration and interval length. The use of these variables by the bat has not been demonstrated. Nor does this finding obviate the possibility that harmonics unique to each individual are used as a basis for recognition.

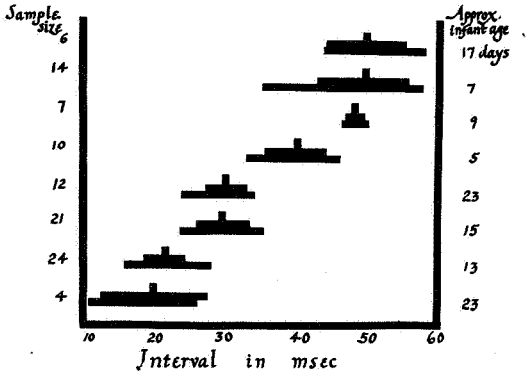

FIGURE 4. Interval from beginning of isolation call to beginning of antiphonal chirp. Symbols as in figure 3.

SUMMARY

Mother-infant pairs of *Myotis lucifugus* were tested for individual recognition using an aluminum sided Y maze. Two mothers were randomly placed at the ends of two of the arms of the maze and the infant was placed at the junction of these arms. The infant's use of vision was eliminated by placing each mother in a holding box which had fine double screening on the end of the box facing the infant. Air was drawn out of the chamber past the two mothers. Twenty runs were completed using 13 mother-infant pairs. The last nine runs were recorded for later analysis of communication signals.

Infants chose their own mothers in 15 of the 20 runs. The authors conclude, therefore, that individual recognition did occur but are unable to determine whether recognition was based on auditory and/or olfactory stimuli. Analysis of the recorded runs shows differences between mother-infant pairs in both

the duration of the infant's isolation call and the interval from the end of this call to the beginning of the mother's antiphonal chirp. Implications of these differences are discussed.

ACKNOWLEDGMENT

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DISCUSSION

WATERMAN: The flying foxes in the Caroline Islands seem to have rather prominent social communication in our audio range. Do these kinds of bats have an echo-locating mechanism?

GOULD: No, but Nelson (ref. 13) has indicated that there is antiphonal calling. He observed the mothers calling to their specific infants; he suggested that they were, in fact, recognizing one another. He did not conduct experiments with individual recognition, although Kulzer (ref. 22) showed that the mother could identify her infant if the infant was in a bag next to a strange infant in a bag. Nelson has described quite a number of vocalizations and has shown how many of them promote spacing in the group since there seems to be in some places limited roosting sites; territorial males are also described.

GRIFFIN: Have you studied the communication calls of the adult bats?

GOULD: Yes. Turner and Shaughnessy put cages a few feet apart and separated them with thick cotton, placing microphones so that only the infant sounds from a single cage were detected. It was rigged with a signal operated relay and checked out on the event recorder to see whether the calling of infants and adults were related. After a long quiet period, the mother would call and then the infant would call, and this would go on throughout the night. They also found that this was true with two different infants. They tried it with adults that were in the colony for some time, and there was no such correlation. A better approach might be to take adults that have been separated for a period of time, where there might be a greater likelihood of communication, particularly those who are closely related or in colonies.

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Neurophysiological Findings Relevant to Echolocation in Marine Animals

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MANY MARINE ANIMALS produce sounds either as vocalizations or otherwise. Theoretically any of these may be capable of providing the basis for echolocation. Even sounds produced from sources completely independent of the animal may be used, as is believed to be true for some blind persons (refs. 1 to 3) and in monaural localization of sound sources in normal people. Whether a given species employs echolocation or in what degree of refinement it employs echolocation cannot be decided from the quality of the sounds available in its environment or from the properties of vocalizations it may produce. Direct behavioral experiment is essential, manipulating the emitted sounds, the echos or the auditory receiving system.

Among marine animals, only porpoises have been convincingly shown to utilize echolocation (ref. 4). Sperm whales and other toothed whales are presumed to use fine grained sonar since they are closely related to porpoises and since they produce click-like sounds resembling the echolocating click of porpoises (ref. 5).

Baleen whales on the other hand are believed not to use a high resolution sonar since they lack such sounds both in respect to the click-like form and the ultrasonic frequencies; they may well detect the bottom and the surface, icebergs and other large objects by echos from their low frequency vocalizations; at least such echos are available as can be appreciated from hydrophone recordings of their calls (refs. 6 to 9).

Pinnipedes, especially sea lions, have been claimed to use sonar (refs. 10 to 18), but most authors have questioned the adequacy of the evidence (refs. 19 to 24).

Penguins have been supposed to use sonar (ref. 25) on the basis of the speed with which they catch fish in the dark! But in the absence of experiments on ear plugging or otherwise interfering with the postulated system the evidence does not yet justify the conclusion. Other swimming birds (loons, etc.) and mammals (otters, dugongs, manatees) are too little known for any significant statements. Although many aquatic reptiles, teleosts, and invertebrates make sounds, none has as yet

been really tested for the use of sonar in publications of which we are aware (ref. 26).

The neurobiologist using only physiological methods cannot say whether a species uses echolocation, either for fine grained object assessment or for simple ranging. He can however hope to discover specializations and differences between species potentially relevant to such accomplishments. He may be able to give clues to the important parameters or stimulus qualities which the nervous system is particularly equipped to discriminate. He may be able to distinguish those parts of the auditory system more likely to be concerned with echolocation than with other kinds of sound analysis, and he may be able to point to structures that act as sound paths, plot receptive angles, and the like.

The first physiological study that undertook these questions on a marine mammal was that of Bullock et al. (ref. 27) on central auditory mechanisms in a series of 29 porpoises, under anesthesia, recording the evoked potential in the midbrain to controlled sounds. McCormick et al. (ref. 28) recorded the cochlear potentials from the inner ear in porpoises. Bullock and Ridgway [1] have studied the evoked potentials in a series of nine unanesthetized, implanted porpoises, and Bullock et al.[2] have studied the evoked potentials in a similar series of sea lions.

COCHLEAR POTENTIALS FROM PORPOISES

McCormick et al. (ref. 28) recorded cochlear potentials from anesthetized dolphins. Up to 100 kHz the slope of the sensitivity curve was found to be similar to Johnson's behavioral curve, but cochlear potentials were recorded as high as 250 kHz. These potentials were used also to test and discard the idea that has persisted up to recent times that the external auditory meatus is a useful and significant route for sound to enter the ear.

EVOKED POTENTIALS IN THE MIDBRAIN OF PORPOISES

Evoked potentials are shifts in the voltage between some point in the brain and a reference electrode elsewhere in the brain or outside of it, time-locked to and elicited by some stimulus under the control of the investigator. The term is generally used for compound potentials representing the activity of many cells as distinct from microelectrode recordings from single units. This is both the strength and the weakness of the evoked potential method. It gives a representative view of the response characteristics of a large sample of reactive units in some proportion to their prominence and synchrony. On the other hand it hides the heterogeneity of neuronal types and displays the algebraically summed field potential from an arbitrary fraction of the population—mixing excited and inhibited, sharply and broadly tuned, simple and complex units. When single units are difficult to get or the adequacy of representation of the whole population of units is in question, the evoked potential can unequivocally show that the central nervous system is sensitive to or discriminates certain stimulus parameters (refs. 29 to 32).

This method has been applied to porpoises using sharpened needle electrodes and fine wires (both however in the "macroelectrode" category)—a single probing electrode in the anesthetized series and arrays of seven to 18 electrodes along a supporting shaft implanted at operation into the brain in the series studied in the unanesthetized state (fig.

[1] BULLOCK, T. H.; AND RIDGWAY, S. H.

[2] BULLOCK, T. H.; RIDGWAY, S. H.; AND SUGA, N.: Acoustically Evoked Potentials in Midbrain Auditory Structures in Sea Lions (*Pinnipedia*). Z. Vergl. Physiol., vol. 74, 1971, pp. 372–387.

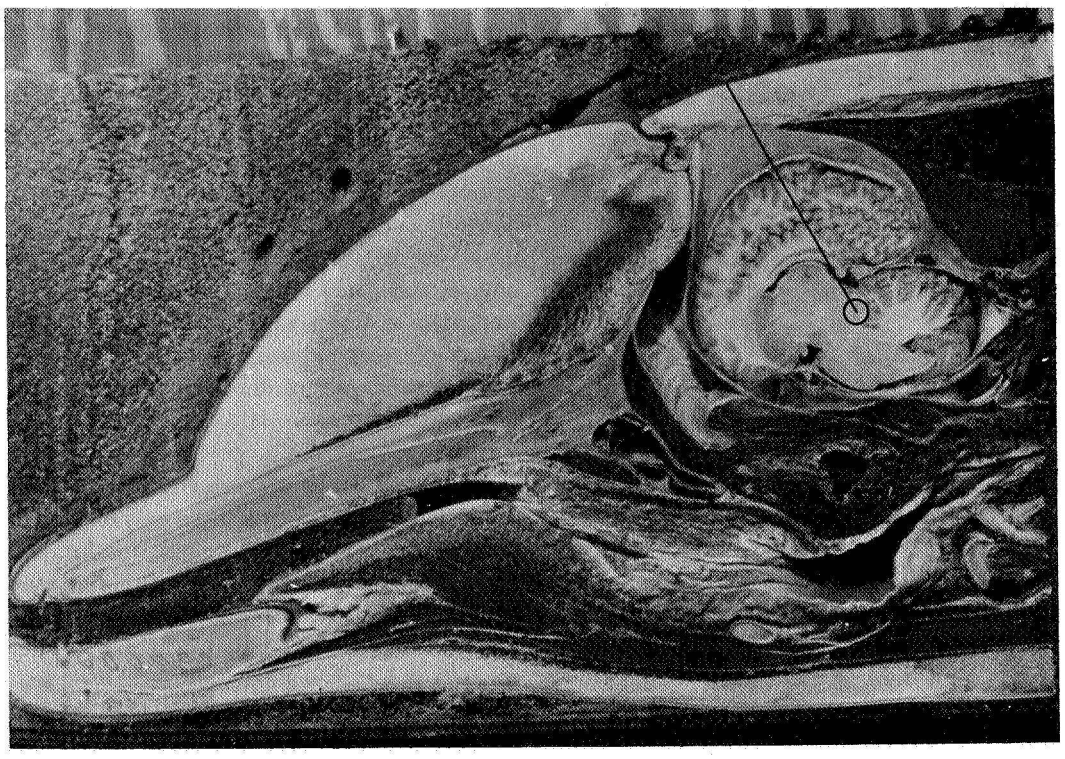

FIGURE 1. Near sagittal section of the porpoise *Tursiops truncatus* showing path of the electrode array used in experiments recording from inferior colliculus. That structure is encircled and is about the size of the circle. Electrode array consists of axial shaft with either seven or 18 independent electrodes of fine wire, one exposed every few millimeters.

1). The electrodes are in each case inserted through small holes in the skull and traverse a good part of the brain in reaching their target, just as in a standard technique used on man and laboratory animals.

Our studies to date on cetaceans and pinnipedes have concentrated on recording in midbrain auditory centers. At higher levels, especially the cortical, the auditory areas are likely to be very extensive and to give more divergent results from experiment to experiment, unless the auditory areas are carefully mapped and landmarks established to permit using the map on each specimen. In addition, our evidence shows that higher levels are more likely to be concerned with more complex auditory processing such as that involved in social communication. These levels certainly need to be studied in future investigations. Midbrain centers, especially the inferior colliculi, are intermediate level centers for analysis of auditory input. They may be specialized to extract information about special features of the stimulus (such as temporal relations, localization in space and the like) to judge from the physiological experience from cats and bats and from general vertebrate and cetacean anatomy (ref. 33 to 37). Although the inferior colliculus is not as spread out as the auditory cortex and the

evoked potentials are more nearly alike from experiment to experiment, it is enormously hypertrophied in the porpoise relative to non-auditory structures in the brain and is no doubt differentiated topographically in ways that remain to be determined in future studies. Our electrodes were sometimes in the nucleus of the lateral lemniscus, a closely related structure on the input side of the colliculus.

Use of Evoked Potentials

Under the conditions of these experiments the electrodes are sensitive to events in a mass of brain tissue at least a cubic millimeter or two in volume so that the properties described are those of a whole region but a quite local region. The form of the potential can be drastically altered by shifting the electrode 1 or 2 mm. An electrode 5 mm from the colliculus may not see any activity in response to sound stimuli even with a considerable amount of averaging of repeated responses.

The inferior colliculus is in the middle of the head and, even though large in cetaceans, is a difficult target to hit blindly with long electrodes inserted through small holes in the skull. This is routinely done with millimeter accuracy in cats and humans where there are prominent skull landmarks visible or palpable from the surface and where atlases and X-ray monitoring are well developed. We used a stereotaxic device built especially for *Tursiops* in order to insert the electrodes into targets located on previous dissections. Due to common asymmetries of the skull and of external landmarks like the blow hole as well as to the difficulty of precise leveling of the head, we felt fortunate, after Dr. Ridgway had accumulated some experience, that he was able to place one or two of the electrodes on each penetration into an active area; that is, a location giving evoked potentials with a good signal to noise ratio in response to sound stimuli.

Figure 2 shows a representative form of midbrain evoked potentials in response to a 300/sec train of clicks. Note that the individual deflections in the evoked potential may be less than a millisecond wide indicating that, although compounded of many unit responses, there must be a high degree of synchronization in a certain population of cells. It also shows the high degree of consistency of the wave form to successive stimuli, giving confidence that details of the complex shape may be significant indicators of sensitivity to stimulus parameters.

The sensitivity of this measure of brain response to subtle aspects of the stimulus is shown in figure 3. Slight alteration of the composition of the short tone burst delivered from a speaker as a result of interposing a thin slip of notepaper close to the surface of

FIGURE 2. Evoked potentials recorded in inferior colliculus during a train of tone bursts, each 0.3 msec in duration including 0.1-msec linear rise followed by 0.1-msec linear decay, composed of 90-kHz sound at −15 dB referred to an arbitrary high intensity, repeated at 300/sec. Loudspeaker and porpoise's head were in the air 75 cm apart (2.2 msec sound conduction time). Sixty-four sweeps computer-averaged. Brief tone bursts every 3.3 msec evoke a potential after latency of 3.5 msec corrected for air time, consisting of a short complex of deflections less than 1 msec wide (ref. 27).

the animal drastically changed the shape of the evoked potential, especially on one side of the brain, even though not attenuating the amplitude of the response. This reversible and repeatable result is dependent upon the exact positioning of the slip of paper over a critical area of the porpoise's head. We do not know whether the alterations in wave

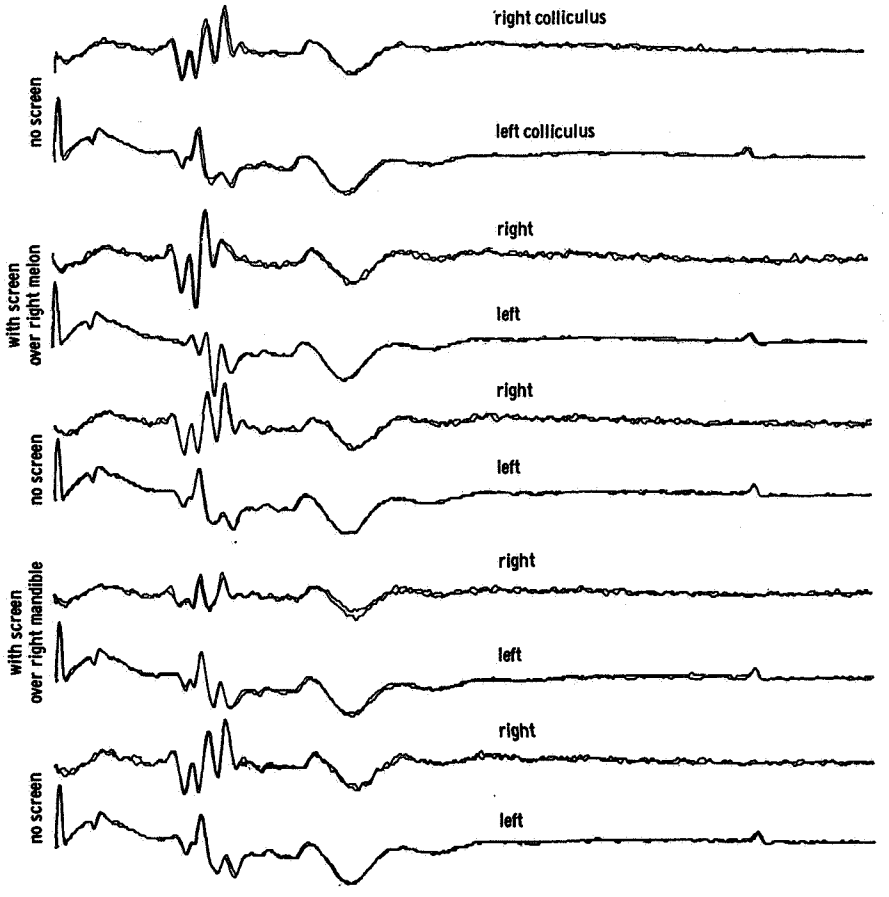

FIGURE 3. Sensitivity of evoked potential waveform to slight distortion of sound. Piece of thin notepaper 10 × 15 cm was held 2 cm from the skin over portion of head indicated. Head and loudspeaker were in the air. Tone bursts of 50kHz, 0.5 msec in duration, and abrupt rise and fall repeated 20 times/sec were delivered by speaker on animal's right. Recording electrodes were in left and right inferior colliculi; deflection upwards represents positivity with respect to an indifferent electrode on the muscle. Slow components of the responses have been filtered out. Sixty-four sweep samples have been computer-averaged for each line; two successive averages are superimposed. Right and left recordings were made simultaneously under each condition. Time of full sweep equals 32 msec. Compared to the form of the evoked potential without the paper screen, the evoked potential on the left side in particular is drastically altered by placing the paper screen over the right melon, but without reduction in amplitude; with screen over the right mandible the form of potential in the right colliculus is most drastically altered. Paper screen position is critical to within a few centimeters (ref. 27).

form are due to recruitment of different populations of nerve cells or to changes in the discharge pattern of given units. It is nevertheless clear that this level in the brain is sensitive to small differences in sound quality.

This is one of the powers of the evoked potential technique since many types of units would not show this sensitivity and only the accumulation of a large sample of many different units would do so. The evoked potential wave form may well be far short of the behavioral discrimination power of the intact animal, but it can still reveal some surprising sensibilities as will be described and ones that are quite relevant to understanding behavioral achievement.

In the typical experiment on the porpoise inferior colliculus, the signal to noise ratio of evoked potentials has been large enough that many features can be distinguished on each individual response. However, for disclosing the differences in waveform to subtler differences in stimulus quality, a number of successive responses, which may be 8 or 16 or occasionally over 100 is averaged on a digital computer thus reducing the relative size of the non-stimulus-locked brain waves.

Sound Path in the Porpoise

The first result that might be mentioned using this technique is shown in figure 4. A small loudspeaker held close to the skin in air or in water or even in contact with the skin reveals that a sound can be more than 50 times weaker and still give a good response if the speaker is held close to the middle of the mandible (on the side opposite the electrode in the brain) than if it is held over the external auditory meatus. If the speaker is held some distance from the animal, it becomes apparent that there is a cone of sensitivity whose center projects from the mandible obliquely forward and down with the sensitivity falling off steeply in all directions around this. From the side, from above, and from very slightly across the midline in front, sound must be much more intense in order to produce a response.

The maximum sensitivity over the mandible supports the speculation of Norris (refs. 38 and 39) of a fat filled canal through the mandible to the middle ear and argues against the proposition of Purves (refs. 40 and 41) and Fraser and Purves (refs. 42 and 43) that the external meatus is functional as a sound path (ref. 27). McCormick et al. (ref. 28) also argue against a functional meatus. Sound enters the head primarily through the skin far forward of the ear and mainly through the mandible, presumably to be conducted through some sound guide to the ossicles of the middle ear. In addition to the contralateral mandible, a second zone of somewhat lesser sensitivity is over the ipsilateral portion of the melon, the forehead-like structure over the upper jaw. Together with the somewhat beamed outgoing cone of energy in the echolocating clicks, the restricted cone of sensitivity to sound on each side could presumably aid substantially in localizing an echo source especially in view of the common scanning movements of the head during closing on a target.

The conclusion that sound enters the body mainly through the skin of the mandibular region and not via the external ear, although based on experiments with four genera (*Stenella, Steno, Lagenorhynchus,* and *Tursiops*), needs to be checked in other taxa especially of the larger whales since it cannot safely be extrapolated to all Cetacea.

Specialization for Ultrasonic Clicks

The second result that should be emphasized is that the response evoked in the midbrain has a great selectivity for the onset of

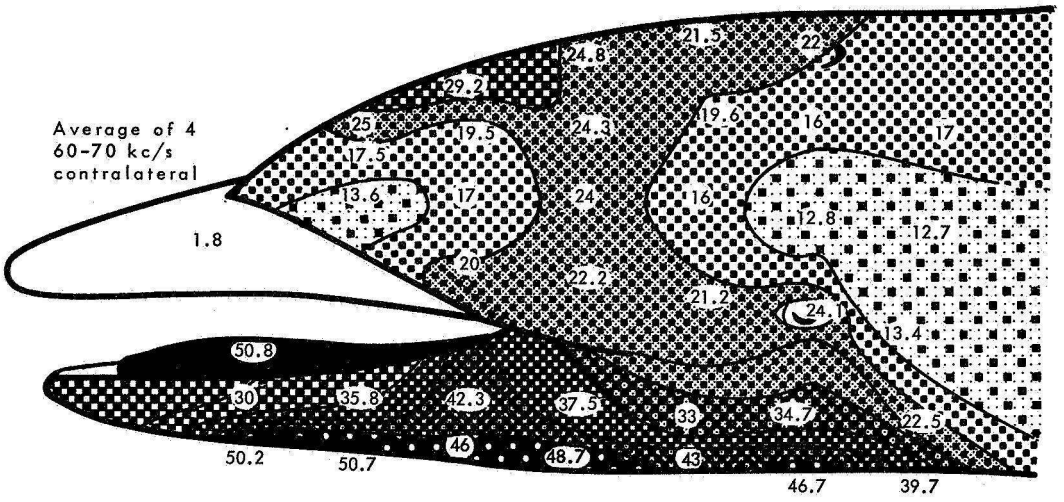

FIGURE 4. Distribution of sensitivity to sound over the head of *Stenella*. Hydrophone was pressed against the skin at points shown. Numerical values represent attenuation at threshold in dB; therefore, largest numbers represent greatest sensitivity. Contour lines are drawn at intervals of 5 dB in sensitivity. Recording was from inferior colliculus on right (contralateral). Sensitivity was greatest along side of contralateral mandible, under tongue, and on ipsilateral melon. External auditory meatus, not shown, is a short distance behind the eye in the area of least sensitivity (from experiments of ref. 27).

steeply rising sound bursts. Using carefully shaped tone bursts with a variable rise time showed not only a maximal response to the most abrupt rise of amplitude of a tone burst, as is usual in other animals, but also a very rapid decline of response as the rise time is lengthened to 0.5 msec. When it is as much as 5 msec, the sensitivity is decreased nearly 100 fold. Even with slow rise times the response is confined to the beginning of a maintained tone, and there is no response in the inferior colliculus by this method to maintained sound. The evoked potential is purely an on-response and under some conditions of strong stimulation an off-response. This is a remarkable specialization in contrast to the cat and, as we shall see below, the sea lion. We shall note that this sensitivity to rate of rise is combined with the capacity to respond discriminatively to different frequencies even in very brief tones and in the first fraction of a millisecond of longer tones. But first we must assess the response area.

Figure 5 shows a number of response areas obtained from different experiments and hence different locations in the inferior colliculus. The best frequencies all lie in the region of 50 to 70 kHz, and the upper limit of response by this method and with our equipment was at least as high as 135 kHz. With equipment that is capable of delivering more energy at high frequencies, it might be found that there is response considerably higher. More remarkable is the lower limit since response falls off greatly below 10 kHz and in most experiments no evoked potential could be obtained in the inferior colliculus with the available energy below 6 kHz. Curves of the same shape are obtained in air and in water.

The curve is of the same shape and even has the same position on the ordinate when steeply rising tone bursts of 0.1-ms total dura-

tion are compared with 1-msec or longer tone bursts. This says that the response to the abrupt onset, which itself is equivalent to a wideband noise burst, does not obscure the specific effect of the frequency contained in the brief tone burst since that frequency determines the high threshold at very low and very high frequencies and the minimum threshold at the best frequency. The response area by the evoked potential technique agrees remarkably well with that measured by behavioral methods by Johnson (ref. 44) in respect to best frequency, upper limit, and approximate dB/octave decrease in sensitivity on each side of the best frequency.

The high best frequency, the very low sensitivity below 6 kHz, the high selectivity for rapid rates of rise of the onset of sound, and the insensitivity to slowly rising or maintained tones are strong indications of specialization of this part of the auditory system for ultrasonic clicks of the echolocating type. The abundant repertoire of whistle-like sounds believed to be important in social communication are chiefly lower in frequency and slower in rise time than our collicular responses demand. (The absence of evoked potentials to slowly rising sound cannot readily be attributed to poor synchronization of units alone, although of course this is possible. The rise times are only a very few milliseconds and elicit good evoked potentials in other animals including sea lions (see below). The number of animals and electrode locations sampled make it unlikely that we have missed a major region of the auditory midbrain, although of course this is possible, too.) One must conclude that the processing and analysis of the low frequency, slowly rising social communication whistles are mainly done elsewhere, presumably at higher levels like the cerebral cortex, and that somehow the streams of impulses for such stimuli get through the midbrain en route to the medial geniculate and cortex too asynchronously or diffusely to produce any substantial evoked potentials. We will return to this remarkable evidence of specialization again below.

Turning to other properties of the responsivity of the inferior colliculus as indicated by its evoked potentials, it is noteworthy that one can easily detect changes in this sign of response to changes of intensity of the sound delivered by as little as 1 dB. Frequency discrimination is also quite sharp, and in some portions of the range a 3-dB change in effectiveness of a stimulus can be caused by a 1 percent change in frequency of the carrier wave in a brief sharply rising and falling burst. Very likely this function is much steeper yet for certain classes of single units.

The response to a given frequency and intensity is markedly altered by the existence of a background tone of another frequency and intensity, especially if these are not far apart or if the background sound is a white noise. Even if it is an octave or more from the brief test tone, there can be a pronounced interaction which is sometimes in the direction of "masking" (i.e., of decreased response to the test tone) and sometimes the opposite, actual enhancement. This relation is complex and frequency specific. The strongly depressing action of white noise raises a serious question as to how the porpoise retains its sensitivity in rapid motion through the water. This rapid motion might be causing masking noise due to turbulence. Perhaps there is a specialization in streamlining and in textural adaptation of the surface of the skin for reduction of such turbulence; if so, the reduction of masking sound may be one of the main achievements of such specialization.

Figure 6 shows that even more effective as stimuli than short pure tone bursts are frequency modulated bursts of the same duration, intensity, and rise time. Over a wide

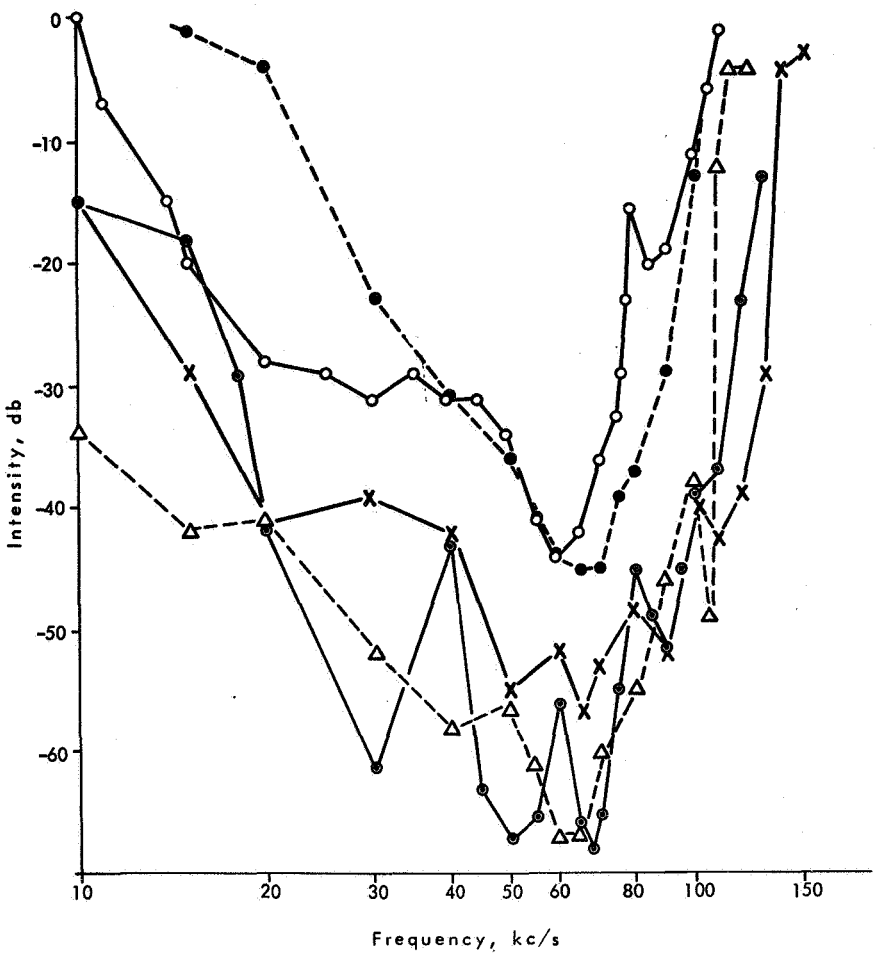

FIGURE 5. Sample audiograms from several *Stenella* made by eye-estimated threshold of evoked potential at each frequency. Intensities are referred to an arbitrary maximum intensity. The peaks of low sensitivity in individual curves are real and presumably represent a patchy or topographically segregated distribution of nerve cells of different response area. Our electrode samples a limited population of cells (ref. 27).

range of frequencies, both ascending and descending, FM typically gives a much stronger evoked response than any pure tone contained in that frequency sweep. Moreover the form of the evoked potential is greatly altered by relatively modest changes in the starting and ending frequency, that is, the span of the FM tone burst. It is not yet known how short a burst or small a span is adequate or what is the optimal stimulus. It is only certain that a small fraction of the FM sweep offered in such an experiment as that of figure 5 is sufficient and has already determined the characteristic shape of the evoked potential for that span.

Recovery of the responsiveness as tested

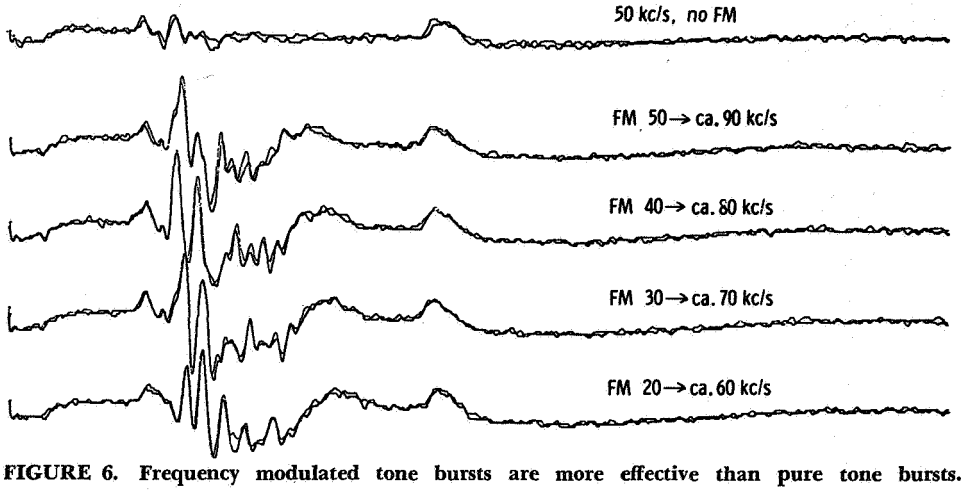

FIGURE 6. Frequency modulated tone bursts are more effective than pure tone bursts. Stimulation by tone bursts 3 msec in duration with 0.5 msec rise and fall. Actually less than 1/10th of this duration is effective, and waveform of evoked potential is determined by a correspondingly small fraction of the 40-kHz range. One hundred-twenty-eight sweeps computer-averaged for each line; two averages superimposed. Time of full sweep equals 32 msec (ref. 27).

by a second stimulus following a first or conditioning stimulus is another sign of specialization for the early echos from nearby objects. Figure 7 shows a sampling of recovery curves from different electrode locations in different experiments. Some show much more rapid recovery than others; evidently some parts of the inferior colliculus are able to show appreciable response within much less than half a millisecond after a previous, nearly maximal response. Figure 7 is based on estimated percentage recovery of a certain landmark in the complex evoked potential form. The actual recovery can be pushed even earlier by computer averaging and subtraction of the response to the conditioning tone alone from the response to the conditioning followed by the test tone. This method shows that there is a small but distinct complex response to the test tone superimposed on that to the conditioning tone even when the silent period between the two 0.1-ms, abruptly rising tone bursts is itself only 0.1 msec. That this is a real recovery is shown by the control in which the silent period is reduced to zero so that we compare a 0.2-ms tone burst with a 0.1-ms tone burst. As expected from the comments previously about the response being essentially an on-effect, there is no appreciable difference between the 0.1- and the 0.2-msec tone bursts. Merely introducing a silent period of 0.1 msec allows sufficient recovery that a new on-response is appreciable and has a complex form, only somewhat simplified from that of more fully recovered responses. We have done experiments where the conditioning tone was nearly maximal in intensity and the test tone many dB lower, as must occur in natural echos. In this case the recovery is significantly slower but is still rapid. Moreover the curve of recovery can have a different form, with some special dips not seen when the test tone is of higher intensity or when it is equal to the conditioning tone (fig. 8).

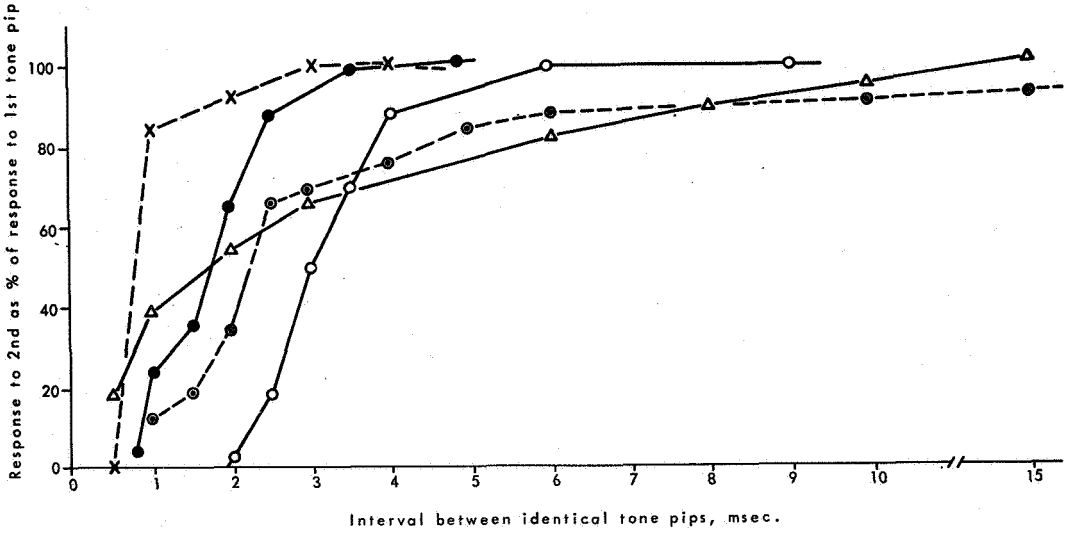

FIGURE 7. Representative recovery curves of collicular evoked potentials in *Stenella*. Two identical tone bursts of approximately 0.5 msec duration and 0.2 msec rise and decay time were given at intervals from 0.5 to 15 msec. Size of the response of certain component to the second of these is plotted as percentage of response to same stimulus alone. Different recording sites show quite different recovery rates, but some are nearly complete in less than 1 msec (ref 27).

Recording with Implanted Electrodes in Alert, Trained Porpoises

All these properties were shown in the anesthetized animals and most of them repeated and confirmed in the unanesthetized, alert, and cooperating animal, as expected from the fact that our anesthesia for the previous work (ref. 27) was a combination of nitrous oxide and halothane. In humans this combination gives complete amnesia for the operation and analgesia, so that the patient does not complain of pain but does understand and respond to commands by the surgeon during the operation.

Still, recording from the unanesthetized and cooperating animal has several justifications besides confirming this expectation. The main one to be reported here is that such an animal, having been trained to do so, can upon command emit a series of clicks like those used in certain kinds of normal echolocation. This gives us the opportunity to study whether the responsivity of the auditory system is in any way different when the animal emits the conditioning clicks voluntarily and hence "knows" when a conditioning sound is going to occur. Furthermore it knows that it will be loud and brief and will probably be followed within a short time by a faint but biologically significant echo. This is potentially a different situation from that we have been describing, in which the conditioning tone is delivered by us at an arbitrary time. The arbitrary time is not entirely unknown or unexpected; if under the conditions of nitrous oxide and halothane the porpoise brain is able to notice, it may perhaps be anticipating the clicks being delivered from our loudspeaker or hydrophone because they are com-

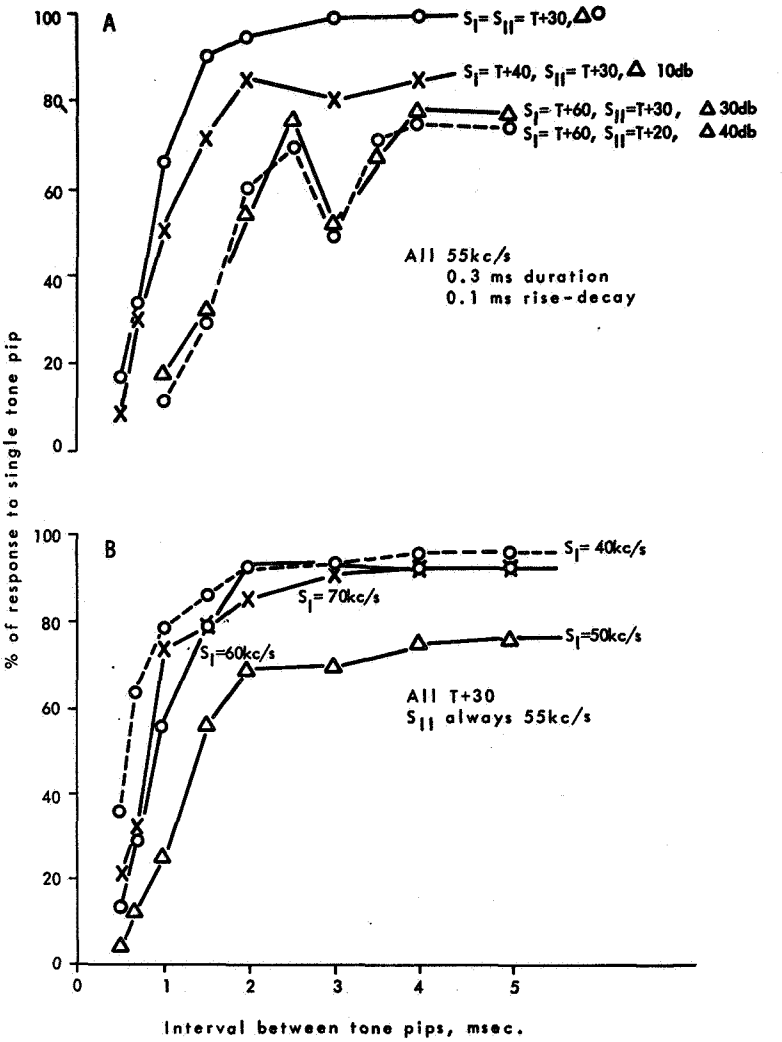

FIGURE 8. (A) Recovery of responsiveness to fainter second stimulus in collicular evoked potentials from *Stenella* with tone bursts of the same frequency (55-kHz, 0.3 msec duration, 0.1 rise and decay times). Recovery of response to the second of the two stimuli plotted as a function of interval, when the stimuli were of equal intensity (30 dB above threshold or T +30), and when the first was 10, 30, and 40 dB louder than the second. Note that although a louder first stimulus does prolong the depression of the second response, recovery is still considerable at 2 msec interval when the first is 40 dB more intense. Note also the dip in recovery curve at 3 msec, presumably representing short-term inhibition superimposed on refractoriness of receptor elements. (B) Comparable measurements showing responsiveness to a 55-kHz signal following exposure at different intervals to an earlier stimulus of 40, 50, 60, and 70 kHz. Both stimuli in the pair were chosen to be 30 dB above threshold at their respective frequencies (ref. 27).

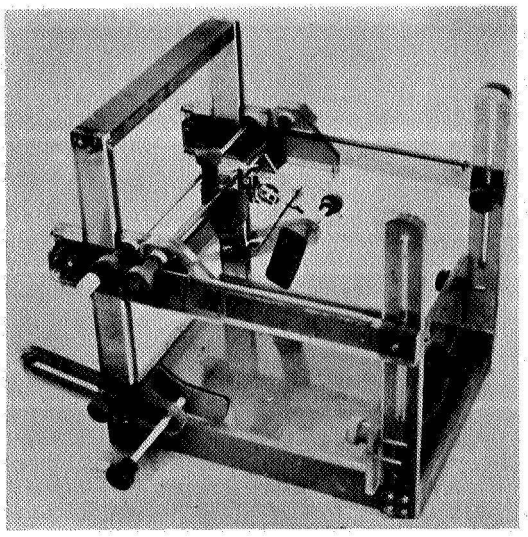

FIGURE 9. Stereotaxic device for porpoises, designed at Point Mugu Marine Bioscience Facility. Porpoise's head enters device from left and is centered and leveled around longitudinal axis by eye. Having chosen the point of entrance relative to surface landmarks like the blowhole, device permits drilling at chosen angle.

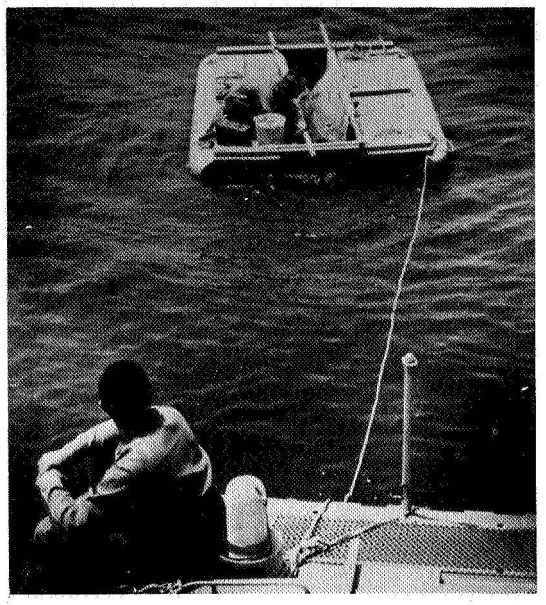

FIGURE 10. Chronically implanted unanesthetized cooperating and trained porpoise (*Tursiops*) lying in a sling in float tethered to research vessel well off shore. Receiving and transmitting hydrophone are attached by suction cups below the water level. Amplifiers held by suction cups above water telemeter the brain potentials to receivers on research vessel. Trainer calls for a series of echolocating clicks when desired (photo courtesy of Pt. Mugu Marine Bioscience Facility).

ing with regularity at a repetition rate well within his normal range, commonly 50/sec.

The implantation of the electrode arrays for chronic preparations is done, usually one on the right and one on the left, each with seven or 18 electrodes spaced from 4 to 10 mm apart along a common shaft. This is the step that requires our stereotaxic device (fig. 9) together with surgery under halothane anesthesia (ref. 45) and X-ray monitoring of the position of the electrode.

Figure 10 shows the animal lying quietly in a sling so that its acoustic environment will be relatively constant, and after hydrophones have been fixed by suction cups to the skin and telemetering transmitters for the brain potentials similarly attached. The recording has usually been done in artificial pools on shore which with high intensity sounds have a complex pattern of reverberation and echo that forms the background on which alterations due to our stimulus conditions are superimposed. Some of the experiments have been done at sea with the animal floating in its sling tethered some meters away from the laboratory vessel carrying the sound generating and recording equipment. There are still many echos under these conditions, but they are far fewer and for the most part delayed sufficiently to be after the epoch of interest for our recordings.

Figure 11 shows the evoked potentials in the inferior colliculus of an unanesthetized, cooperating, and trained animal in response to his own voluntarily emitted clicks. Such records have shown among other things a remarkable lack of parallelism between the

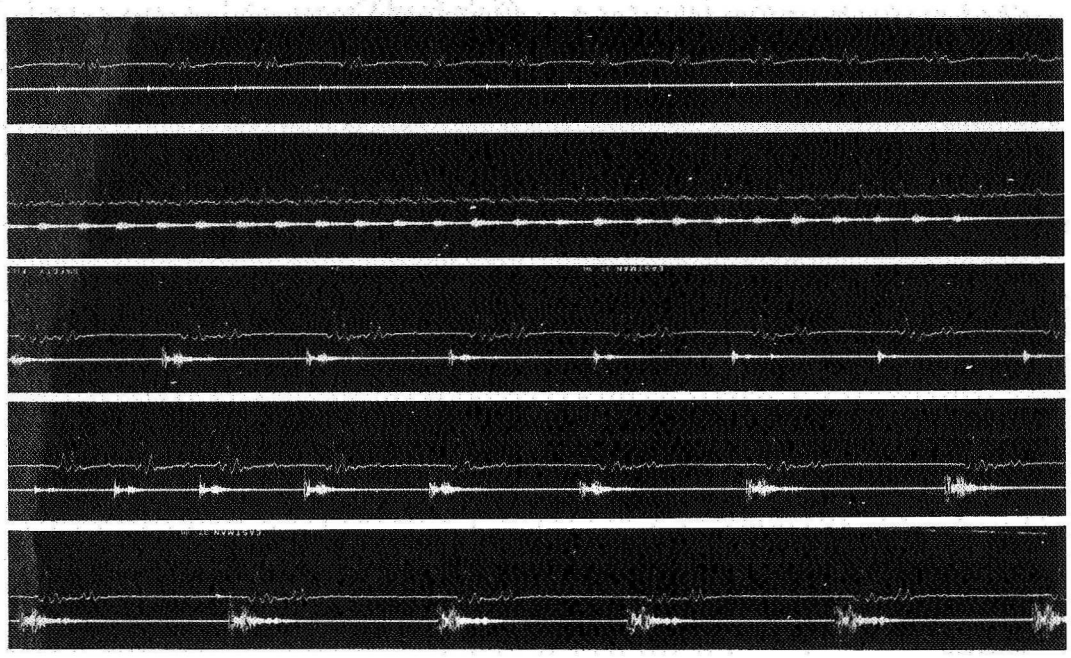

FIGURE 11. Evoked potentials (*upper trace*) from inferior colliculus or vicinity in an alert, cooperating, trained porpoise (*Tursiops truncatus*), implanted several days before, with 14 electrodes, in two linear arrays or assemblies, one left and one right, each of 7 fine wires emerging and bared at staggered intervals of 5 mm from an insulated hollow needle. Running film record from magnetic tape of the experiment. Brain potentials are responses to sounds produced voluntarily by the porpoise and recorded by a hydrophone (*lower trace*). Note that some low amplitude sounds produce sizeable evoked potentials and some high amplitude sounds small potentials. Shown are non-consecutive samples from several different click trains. Each line is 200 msec long.

variations in amplitude of the emitted clicks as seen by a fixed hydrophone and of the recorded evoked potentials. Some very intense clicks of the long (1 to 2 ms) type are accompanied by modest evoked potentials. Many feeble clicks, 20 dB weaker, of the short (0.06 to 0.2 ms) type evoke good brain responses. It appears that some component of the emitted clicks is important for the response in the inferior colliculus and that this component does not vary in amplitude *pari passu* with the variations in overall intensity of the click.

If we compare the size of the response to a voluntarily emitted click with that to a sound we deliver of the same intensity as seen by a hydrophone near the head, the latter is a much smaller evoked potential. From our experience with different kinds of sounds we believe this discrepancy cannot entirely be attributed to the quality of the porpoise's own click, but we cannot be certain of this. Presumably, therefore, we are seeing a more effective click due to its greater intensity inside the head. This would be evidence, no stronger than the certainty of the exclusion just proposed, that the inner ear and the sound guide to it are not perfectly isolated

acoustically from the sound-generating parts of the head (refs. 40 and 41). Therefore, we cannot tell whether the response to his own clicks embodies some self-protection from the expected loud sound.

When we use the animal's voluntary click, as recorded in a hydrophone close to the head, to trigger our sound generator to deliver a test sound from another hydrophone acting as a loudspeaker, we can test the responsiveness at chosen delays after the animal's own click with what amounts to artificial echos. They have the important advantages over natural echos that the test tone burst is constant in form, composition, and intensity whereas the natural echos are inconstant both because of variations in the outgoing click and because of slight movements of the head or of the target. Figure 12 shows one such experiment with artificial echos at various intervals. The principal result is that in comparison with the recovery of responsivity following conditioning sounds delivered arbitrarily by us, recovery is not greatly different under our conditions. There is no supernormal or facilitated period, but recovery

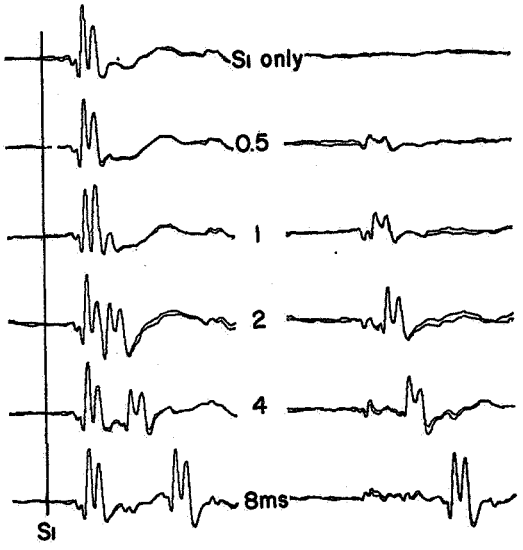

FIGURE 12a. Rate of recovery of evoked potentials from an animal and electrodes like those in preceding figure. Computer-averaged records. Experiment shows recovery after a response to a "conditioning" stimulus (S1), as revealed by response to subsequent "test" stimulus (S2), after different delays. Upper: S1 and S2 are both artificial tone bursts of 50-kHz, 0.2 msec duration, abrupt rise and fall, about 30 dB above visible evoked potential threshold, without averaging. Two independent averages of 32 sweeps each are displayed. On left are records of both S1 and S2 responses; right are results of subtracting the S1 response alone from each of the pairs, to uncover the component attributable to S2.

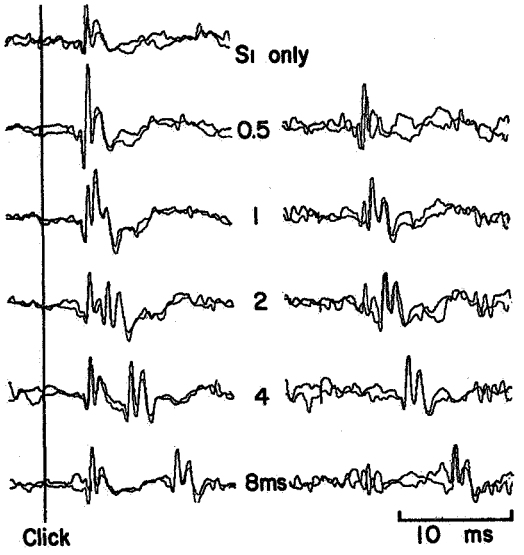

FIGURE 12b. S1 is a click in the porpoise's own train of echolocating clicks, spontaneously emitted when a fish is tossed into the pool 2 m from his snout; clicks used here are one of his very brief, medium intensity type, the single main wave having a duration of 0.1 msec. S2 is an "artificial echo," like the tone bursts of the upper half. Successive porpoise clicks triggered the sequence, 0.5, 1, 2, 4, 8 msec delay and no S2, over and over to provide records for averaging. Two independent averages of eight sweeps each are displayed. Comparison, especially at 0.5 and 1.0 msec, indicates better recovery following porpoise's own click, though it may help that click and test echo are not identical sounds.

is at least as good, perhaps somewhat faster, following the animal's own voluntary click. This is cautiously stated because we cannot compare conditioning bursts exactly matched in quality or even in intensity with porpoise clicks, since the latter reach the ear partly through the head. But the extremely conservative comparison of equal conditioning and test tones with porpoise clicks causing substantially larger evoked potentials than the artificial echo sound by itself shows no less but apparently more recovery at the earliest interval of 0.5 msec after the porpoise's own click (fig. 12).

It will be interesting to pursue these matters also in the case of high repetition rate clicking by the porpoise when echos from objects 2 or more meters away will be returning, not in the interval between that click and the next but in a subsequent interval (refs. 32 and 46). Insofar as the repetition rate of clicks rarely exceeds 500 to 700 per sec and recovery is very well along though not complete in that interval, it is quite feasible physiologically for echos to be analyzed during the high frequency buzzes or squeals. Figure 13 shows a sample of such a buzz and of other epochs when sounds of different kinds occurred. Note that many kinds of sounds including the porpoise's own whistles do not cause evoked potentials in our electrodes, emphasizing once more the specialization of this region of the auditory system for echolocating clicks. On present evidence it seems reasonable physiologically that the porpoise can measure distance and at the same time evaluate the character, size, and location in space of an echoing object (ref. 47).

Evoked Potentials from the Cerebral Cortex in Porpoises

Finally it should be reported that although we have made no systematic study of the responses from the cerebral cortex, on a few occasions we recorded from a cortical site far ventrally and laterally and obtained responses to sounds quite different from those in the colliculus. Slowly rising and maintained sounds as well as low frequency tones extending below 1 kHz elicited good responses similar to familiar cortical-evoked potentials, and the best frequency was about 5 kHz. It appeared that we had found the missing portion of the auditiory system specialized for analysis of the low frequency social communication whistles that cause little or no response in the colliculus.

AUDITORY EVOKED POTENTIALS IN PINNIPEDIA

Because they belong to quite a different order of mammals and yet face the same problems and opportunities in the aquatic environment as do porpoises, we have made a parallel study of a series of ten sea lions (*Zalophus californianus*).[4] The basic technique was the same as for the porpoises. We used chiefly barbiturate anesthetized animals since these species do not lie so quietly or tolerate attached loudspeakers or hydrophones so well as porpoises. From data on cats this anesthetic should exert little or no effect upon evoked potentials at the level of the midbrain. We have done some experiments on unanesthetized, restrained sea lions however and have seen no difference in the results. Recording and stimulation have been done in air and under water with no obvious differences.

The results of principal interest are the following. The upper limit of frequency to which evoked potentials could be obtained with the intensities of sound available was 30 to 40 kHz in different experiments. This con-

[4] BULLOCK ET AL., *loc. cit.*

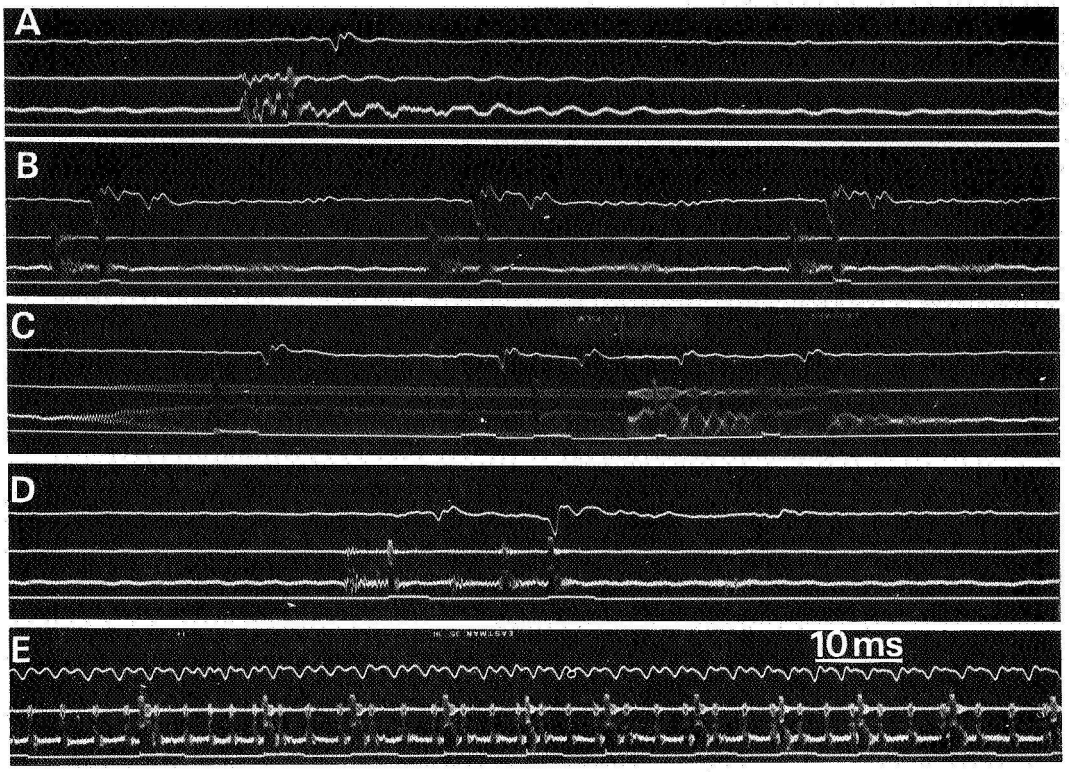

FIGURE 13. Evoked potentials (*upper trace*) from an animal and electrodes like those in figure 11. Running film record from magnetic tape of the experiment. Two *middle traces* are hydrophone outputs at low and high gain showing "artificial echos" or test tone bursts (marked by the ON of the square wave in *lower trace*) delivered at chosen intervals after trigger pulse produced by onset of porpoise's own echolocating clicks (*B*, *D*) or some of them (*E*) or by some other sound (*A* and *C*). *A* shows that a sound of low frequency (second and highest deflection = about 4 kHz) relative to the clicks and test tones (main energy about 20 and 40 kHz, respectively) is ineffective in eliciting an evoked potential; single evoked potential in this line serves as a control—the response to the test tone alone. *B* shows three clicks of high intensity, long duration (>1 msec) type, followed by "artificial echos" after 6 msec. Evoked potentials follow both sounds with a latency from hydrophone deflection to collicular deflection of 4 msec and show complete recovery of responsiveness (compare *A*). *C* shows that the porpoise's own social communicating whistles (about 3 to 6 kHz) do not evoke any potentials or seriously mask response to test tone. *D* shows an ineffective sound of too low a rise time and frequency, followed by effective test tone, and effective click followed by poorly recovered test tone response. *E* is sample of high repetition rate clicking ("rusty hinge" sound; 250 to 350 clicks per sec) with intermittent test tone bursts; these are followed at the expected time (4 msec) by partially recovered evoked potentials superimposed on those to the clicks. This is the situation during high resolution discrimination by the animal of targets close by, though with echos that follow every click. The test tone, though higher in amplitude, is not as effective as a porpoise click (or its echo) presumably because it does not have the best frequency-succession (FM); it is a 40-kHz tone, 0.6 msec long, rising and falling abruptly, about 30 dB above visible evoked potential threshold without averaging. Each line = 125 msec.

trasts with Mohl's figures (refs. 48 to 50) of 64 kHz or higher for the seal (*Phoca vitulina*) by behavioral end point (ref. 51). The evoked potentials in the inferior colliculus in sea lions respond maximally to abruptly rising tone bursts but decline relatively little as the rate of rise of the tone burst is lengthened. Excellent responses are obtained with 50 msec and even slower rise time. The response is still chiefly a transient one however. There is no marked advantage in effectiveness of frequency modulated stimuli over pure tone stimuli whether upward or downward. The best frequency is below 5 kHz, and responses have been obtained as low as we have looked, which is about 0.6 kHz. The frequency and intensity discrimination is not nearly as good as in the porpoise. Recovery of response after a conditioning tone is appreciably slower than in porpoises and appears similar to that reported for cats. Typically 50-percent recovery is obtained by 2 or 3 msec. With protracted averaging of several hundred responses and computer subtraction of conditioning response from conditioning plus test response, it is possible to see a small response to the test click when only 0.2 msec of silence has occurred since the conditioning click. There is very little directional sensitivity (ref. 52), and the response is obtained in all 360° in the horizontal plane around the head with only an advantage of about 10 dB for a hydrophone held 10 cm lateral to the contralateral external ear, over the least effective positions which are almost equally behind the head, straight in front, and to the side of the ipsilateral ear. These figures are of course very rough and depend on many factors in the stimulus situation but serve to emphasize their dramatic difference from the porpoise's limited cone of receptivity with its best direction not to the side but only 10° or 15° from the midline straight ahead.

In sum, the pinnipedes examined have auditory responses like those of a cat gone to sea with little evidence of porpoise-like specialization. This agrees with the report of Alderson *et al.* (ref. 53) on the cortex of *Phoca*. The inferior colliculus, of course, responds very well to sharp clicks such as would be particularly favorable for echolocation and have been reported by some observers to be emitted on occasion by sea lions, but their system cannot take advantage of ultrasonic frequencies, of frequency modulation, or of small differences in frequency to nearly the same extent as can porpoises. Nor is the inferior colliculus as clearly specialized for brief high frequency clicks as it is in porpoises, but it responds quite well to low frequency, slowly rising sounds such as those involved in social communication.

COMMENT AND FUTURE PROBLEMS

These studies on porpoises and sea lions bring out aspects of specializations that distinguish the two groups in auditory analysis of sounds. The specializations help to explain how the fantastic achievements of the porpoise in recognizing and localizing small targets of very slight difference in echoing quality (refs. 54 and 55) can be understood in neurophysiological terms. It is not possible on these purely physiological data to pronounce on the question, still debated in the literature, whether sea lions and other pinnipedes use echolocation. We can, however, say that sea lions are relatively unspecialized compared to porpoises.

Dr. Griffin likes to ask why we can't do what a bat or a porpoise can do. If our own system is more like a cat's and hence a sea lion's, these findings on central specialization help to explain it. Nevertheless many questions remain to be investigated. For example, what electrophysiological signs and measures can be found of ability to localize echoing

objects, static or moving, and are they specialized compared to ordinary mammals? Is there any neural facilitation of expected echos? Are middle ear muscle reflexes employed to depress responses to the animal's own outgoing click and yet be ready for early returning echos in the rapidly sound conducting aquatic medium? For what does a porpoise need the tremendously enlarged inferior colliculus; what can he do that requires so many neurons? The inferior colliculus alone is larger than a whole bat's brain, indeed nearly as big as some small bats. What is the function of the inferior colliculus in the baleen whales that apparently lack the ultrasonic click emissions and presumably the fine grained echolocation of the porpoises and toothed whales? What types of units account for the responses in the inferior colliculus of porpoises, and how do they differ from those in cats and sea lions? What happens in the medial geniculate? Where and how extensive is the auditory cortex in toothed and in baleen cetaceans, and how is it organized and specialized compared to cats and other laboratory animals?

The studies reported show that, given the specimens and the facilities, the techniques are now perfectly practicable to anticipate resolution of all these problems.

SUMMARY

Recent work is reviewed, chiefly on porpoises, showing peripheral auditory and central neurophysiological specializations favorable for the analysis of echolocating clicks and their echos.

As seen in the cochlear potentials as well as in evoked potentials of the midbrain, the upper limit of reception extends at least to 135 kHz and possibly higher. Best frequencies for evoked potentials in the midbrain are in the range of 50 to 70 kHz.

Sound is received mainly through the skin of the mandible, and the sensitivity over the external auditory meatus is very much less and no better than surrounding areas of the head. A region of somewhat less sensitivity than the mandible but higher than elsewhere is over the melon. There is a restricted cone of receptivity extending forward and downward, with a center 10° or so from the midline of the head and falling off steeply so that sound from a source 45° to the side may be 20 to 30 dB less effective.

One of the auditory stations, the inferior colliculus, is enormously hypertrophied and from its evoked potential highly specialized for rapidly rising sounds of high frequency and short duration. It has given all the response it will to a tone burst of less than 0.1-msec duration, but longer durations give no greater response. It is extremely sensitive to the rate of rise in the 0.05-to 2-msec range, and a tone of 5-msec rise time is nearly one hundred fold less effective than an abrupt tone. In spite of listening for such a short period, the inferior colliculus makes extraordinarily fine frequency and intensity discriminations. It responds better to frequency modulated than to pure tones, again discriminating sharply between slightly different FM tones. It is strongly and complexly subject to interactions with other tones in the background, some of which mask and some of which actually enhance the response. Recovery is very rapid even when the second or test sound happens to be very much weaker than the first.

The evoked potential from the midbrain sites studied is remarkably insensitive to low frequencies (below 6 kHz) and to slowly rising amplitude (above 5 msec). It manifests a system highly specialized for echolocation clicks. The slower and lower sounds like those in porpoise whistles do evoke responses in the cerebral cortex.

These properties have been confirmed in unanesthetized, alert, and cooperating animals with implanted electrodes. This technique has permitted recording the evoked potentials in response to the animal's own voluntarily emitted echolocating clicks delivered both in response to objects of interest like fish thrown into the water and after training to deliver clicks in response to the trainer's command. Such evoked potentials suggest that some component of the click is most effective in eliciting these responses—a component that does not necessarily vary in proportion to the overall intensity of the click. They also suggest that the inner ear and its sound path are not perfectly isolated acoustically from the sound generating parts of the head since the evoked potentials are much larger than those to artificial sounds of the same intensity as seen by a hydrophone near the head of the animal.

Extending this technique to use the animal's voluntary echolocating clicks, picked up by a hydrophone, to trigger a sound generator that delivers an artificial echo after a chosen delay has permitted examining the recovery of responsiveness to the standard test tone as a function of time after the outgoing voluntary click. Recovery is found to be at least as rapid as for artificial sound, probably more rapid, but no facilitation has been seen under our conditions.

In all these respects the responses obtained in a comparable way from the sea lion show much less specialization for clicks and their echos. The responses of the sea lion are very much like those of cats. The upper frequency limit of sensitivity is between 30 and 40 kHz with available intensities.

Other vertebrates and invertebrates are still too little known to make meaningful statements on the neurophysiological properties that might be relevant to any echolocation of which they are capable.

ACKNOWLEDGMENT

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DISCUSSION

NORRIS: Have you seen any evidence in the records of the animals hearing their own signals as they are emitted, and before they return as echoes?

BULLOCK: Frequently. They respond to their own sounds. The first big wave that you see is a response to his own sound. Of course, I can't say whether that is mediated through the water or whether he is just getting the sound in the inner ear before it ever gets out to the water. What we are particularly interested in is whether the animal is perhaps quite insensitive to this, or at least less suppressed by the loud outgoing sound when he does it himself. He knows when it is going to happen, knows that it is going to be loud, and knows that it is going to be brief.

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A Theory for the Function of the Spermaceti Organ of the Sperm Whale

(*Physeter catodon L.*)

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WITHIN THE SPERM WHALE FOREHEAD lies the spermaceti organ, occupying as much as 40 percent of the entire length of the whale. It is a huge, somewhat flattened, cone-shaped structure. It is covered dorsally and laterally by a thick wall of intermeshing ligamentous cables, many as thick as a man's thumb. In the day of the hand whaler, this stout outer structure was called "the case." The organ is filled in life with as much as 1900 liters of a liquid, or semiliquid waxy oil, the spermaceti—the material once so prized for candles and illuminating oil. Surrounding this organ at either end and below are air sacs, which are part of a complicated series of highly asymmetrical nasal passages, valves, and associated structures. The functions of this complex have been subject to some speculation. See discussion in Appendix. Also, Raven and Gregory (ref. 1) speculated that the case and its contained spermaceti "is to make diving possible by firmly closing the outer and inner nasal passages." They go on to say:

> We infer that its main function is to act as a force pump for the bony narial passages, drawing a great quantity of air into the respiratory sacs and perhaps preventing the escape of air under the pressures of the great depths. It may also act in part as a hydrostatic organ since by severe contractions of part of its muscular sheath, the contained oil might be squeezed toward one end or the other, while the air sacs were being inflated, thus lightening the specific gravity of that end and tending to alter the direction of motion of the animal.

It is difficult to interpret exactly what Raven and Gregory mean by a "force pump," but we assume it means that movements of the spermaceti organ are capable of drawing air out of the posterior air spaces (lungs, trachea, head canals, middle ear) into the nasal sacs of the forehead. The idea,

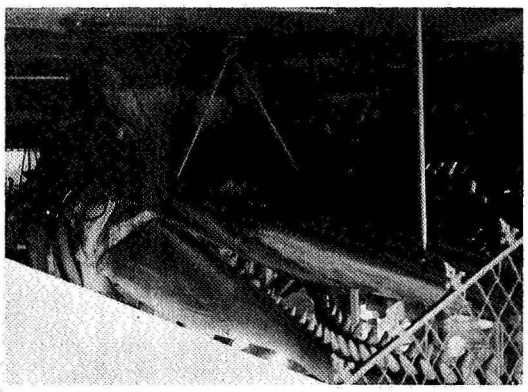

FIGURE 1a. Sperm whale skeleton at the Museum of Comparative Zoology, Harvard University. Note the low channel-shaped rostrum and the amphitheatre-like forehead. The spermaceti organ lies above the rostrum and is bounded posteriorly by the frontal sac which tightly adheres to the amphitheatre walls. Photo courtesy William Schevill, Harvard University.

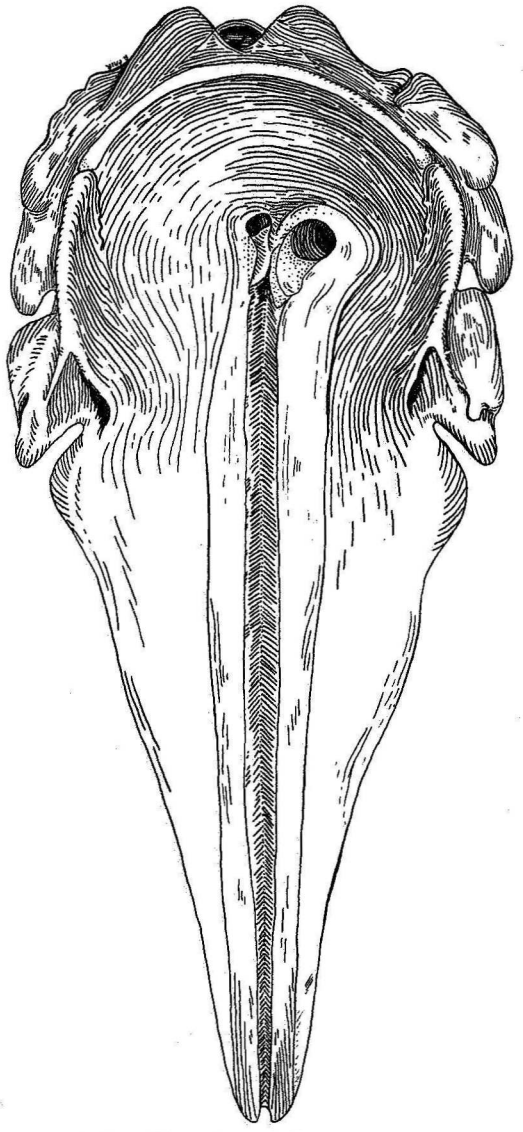

FIGURE 1b. Plan view of the sperm whale skull showing the asymmetry of the superior bony nares and their disparate sizes—from skull in Los Angeles County Museum.

we assume, is that such additional air in the nasal sacs of the head when under pressure would serve to close the nasal passages enough to prevent air loss under the pressure of diving. The ideas are certainly partly incorrect for reasons we will discuss later, and the suggested functions seem unlikely. However, we do not discount the possibility that the musculature of the forehead may be involved in a cycling of air within the sac system of the forehead.

This paper presents a new theory for the function of the complex as a whole and brings forth some supportive evidence for our views. Briefly we suggest that (1) the spermaceti organ is an acoustic resonating and sound-focussing chamber used to form and process burst-pulsed clicks; (2) the nasal passages of the forehead not only allow the repeated recycling of air for phonation during dives, but provide mirrors for sound reflection and processing; and (3) this entire system allows sound signal production especially useful for long-range echolocation in the deep sea.

To show the basis for these ideas, we will first examine the pertinent details of anat-

omy, then review what is known about the sounds of sperm whales, presenting at this time some new data, and then draw these facts together into a coherent theory. Finally we will describe a model of the sperm whale acoustic system with which we have produced simulated sperm whale signals. This simple apparatus, which was built using engineering design criteria we see in the animal, produces remarkably similar signals to those recorded from living whales.

During the course of this work, two fetal sperm whales were examined, an adult was dissected, and various samples obtained for histologic analysis. The species was observed and recorded at sea on three occasions. Various observations and measurements have been made on museum skeletal material.

These ideas were conceived nearly 4 years ago and opportunity to test them has been sought since that time. It has not come easily, so the information is presented at this time, incomplete as it is, in hope that others may be able to contribute.

The ultimate proof, rejection, or refinement of our ideas must probably await experiments on living sperm whales, but we feel that our information is sufficiently advanced and documented to make it useful at this time, especially in view of the rarity of opportunity to work on living examples of this species.

THE ANATOMY OF THE SPERM WHALE FOREHEAD

The Skull

Perhaps the most noteworthy aspect of the sperm whale skull is the amphitheatre-like, nearly parabolic forehead and the broad low rostrum extending forward from its base to the tip of the snout (fig. 1A, 1B). Because the slim elongated tooth-bearing lower jaw is wholly ventral, like that of a shark, and the rostrum lies above it, the great majority of the huge forehead of the whale is composed of soft tissue.

The bony nares pierce the rostrum near its base and are highly asymmetrical. At the surface of the rostrum in adult whales, the right naris is approximately one-seventh the cross-sectional area of the left naris and is located on the midline lying almost equidistance from all points on the curved amphitheatre (fig. 1B). This amphitheatre is formed largely by the premaxillary, maxillary and nasal bones. The larger left naris is well displaced to the left.

In the living animal, the bony amphitheatre is covered over most of its area with the tightly adhering posterior wall of the frontal sac, a diverticulum of the right nasal passage. The bony rostrum, which in coronal section is shallowly dish-shaped (fig. 1A), is filled by the "junk." Junk is an old whaler's term for this fatty mass, tightly bound in connective tissue, that was less valuable than the spermaceti. It is separated from the spermaceti organ above by a broad channel-shaped anterior branch of the right nasal passage.

Spermaceti Organ and Nasal Passages

The spermaceti organ extends posteriorly from just beneath the tip of the snout to the anterior skull amphitheatre. The great relative length of the organ is accounted for in part because the snout of adult sperm whales overhangs the upper jaw by about 5 percent of the total length in adults (ref. 2). The spermaceti organ is bounded at both ends by the large vertically oriented air sacs mentioned above. The ligamentous case surrounding the spermaceti organ is extremely stout and difficult to pierce even with a sharp knife. When one does penetrate this layer

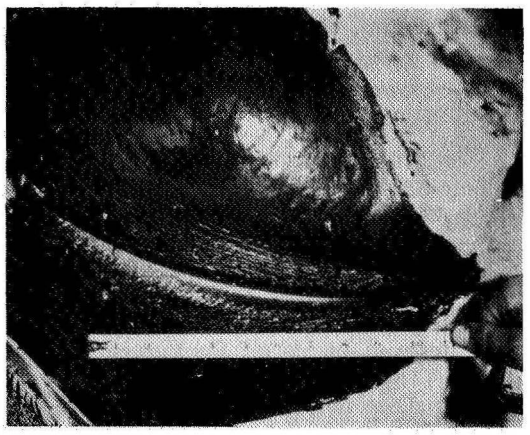

FIGURE 2a. ***Museau du Singe,*** **or monkey's muzzle, of an 11-m sperm whale dissected at Richmond Whaling Station, California. Whale has been cut through the anterior snout at the point of inflexion above the upper jaw and the distal sac reflected from the museau lips. In lower left corner note triangular band that normally rests between the lips of the museau. Bulbous upper lip of the museau is actually the anterior extension of the spermaceti organ, and the lips cross its entire width. Rule in inches.**

during dissection of a fresh specimen, liquid spermaceti exudes forth as if under considerable pressure.

To describe the organ in more detail, it seems best to start from the anterior end of the animal and work posteriorward to the amphitheatre of the skull. The anterior surface of the sperm whale snout is strongly indented both laterally and transversely across the whale's forehead a few inches above the upper jaw, and flares out above into the bulbous forehead which bears the asymmetrically placed single S-shaped blow hole on its anterolateral surface.

If one makes a horizontal cut into this indentation, very dense connective tissue is first encountered, which is much thicker above and below the indentation. After penetrating a centimeter or two through this tissue, the distal sac is encountered, which spreads across the width of the snout. By reflecting the walls of this sac, the *museau du singe*, or monkey's muzzle (fig. 2A), is exposed (see refs. 3 and 4). This structure consists of a pair of extremely stout black lips, occupying nearly the entire width of the posterior wall of the distal sac (fig. 2B). They close the anterior end of the right nasal passage.

The spermaceti organ ends anteriorly in the upper lip of the *museau du singe* as a very flattened oval of liquid-filled space that gives way anteriorly to more tightly bound lipid material and finally to dense connective tissue within the upper lip. The organ becomes much deeper as one explores posteriorly, in the form of a wedge, curving slightly over the junk until it reaches the amphitheatre of the skull. There its posterior wall consists of a smooth, nearly circular, vertically oriented wall that forms the smooth anterior face of the frontal sac. This wall looks very much like the head of a bass drum, although it is much more flaccid, and one may press it inward with a modest pressure of the thumb.

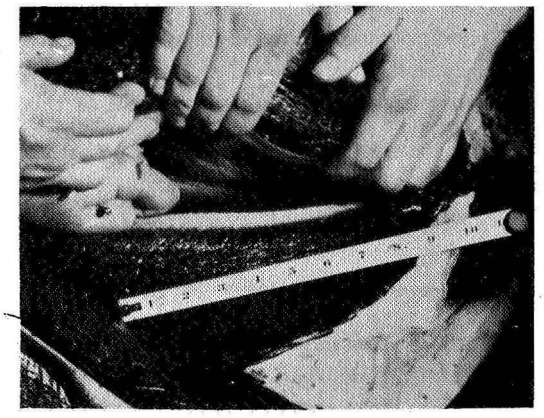

FIGURE 2b. Pulling museau lips apart requires considerable force. Notice cornified band between two hands on right and black grooves behind.

Looked at in their totality, the nasal passages form a nearly horizontal U-shaped loop, formed of sacs and canals, running from one bony naris forward to the tip of the snout and back again into the other bony naris (fig. 3). At its left anterior corner, this loop is pierced by the S-shaped blowhole. If we follow this loop around, starting at the right bony naris, first encountered is a muscular valve that is presumably capable of closing the right naris. Dorsal to this plug, the right passage bifurcates and one branch extends nearly vertically and expends into the frontal sac. This sac covers nearly the entire anterior face of the skull amphitheatre (fig. 1A).

The other branch enters between the junk

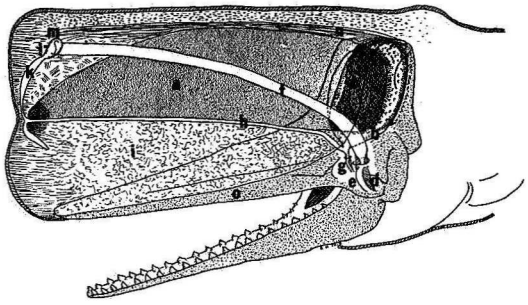

FIGURE 3. General diagram of nasal passages and spermaceti organ of sperm whale forehead. Oblique view to show relative positions of right and left nasal passages.

- **A. Spermaceti organ**
- **B. Frontal sac**
- **C. Skull amphitheatre lined with fluid-filled knobs**
- **D. Pterygopharyngeus muscle**
- **E. Left bony naris**
- **F. Left nasal passage**
- **G. Right bony naris**
- **H. Right nasal passage**
- **I. Junk**
- **J. *Museau du Singe***
- **K. Distal sac**
- **L. Connecting sac**
- **M. Blowhole**
- **N. Ligamentous case**
- **O. Rostrum**

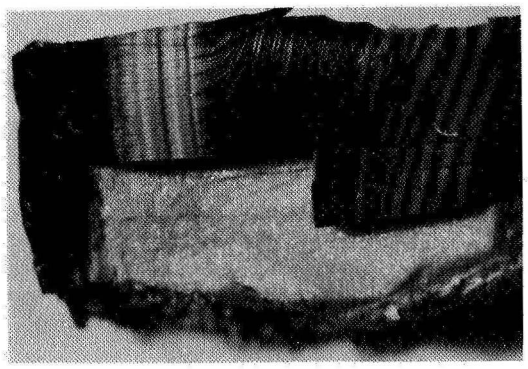

FIGURE 4a. Section cut through lower lip of *museau du singe* of an 11-m sperm whale, showing the blackened grooves behind (right) that swing perpendicular to cornified band that arcs along lip border. Note three raised ridges of the band and two grooves, and also the fine hair-like extensions of the grooves that cross the cornified band. At left is seen the stiff crenulated tissue of the distal sac found above and below the museau lips.

and the spermaceti organ and passes forward as a broad thin-walled horizontal sac. Near the tip of the snout, it narrows and passes between the lips of the *museau du singe*. Posterior to the *museau* the sac walls, both above and below, are marked by a peculiar group of numerous approximately parallel black lines that curve across the sac at roughly right angles to the body axis on both dorsal and ventral sac walls, as mirror images of one another (fig. 4A). They then turn and run along the trend of the longitudinal body axis for a short distance before reaching the posterior edge of the curving *museau*. They are so arranged that at the posterior border of the lips they are spaced with great regularity across the arc of the lips approximately 0.05 mm apart in our specimen. If one views these lines in reflected light, it is at once obvious that they are not simple pigmented stripes but actually shallow grooves that become deeper (0.03 mm) as they approach the lip

FIGURE 4b. Cross section through the museau of the same whale. To the left (a) are blackened grooves cut obliquely. At (b) note the very thick pellucid cornified tissue of the lip band. Grooves and ridges are not very evident in cross section.

border (fig. 4B). The groove profile is saw-toothed where the grooves cross the width of the sac. Thus, if one moves a dissecting needle anteriorly across the sac wall, a broad interspace between grooves is first encountered, and the needle then moves downward into a groove whose anterior wall is an abrupt face. The grooves on the upper and lower sac walls are mirror images of one another and thus, when the sac walls are pressed together, a series of tubelike curving channels probably results. Fine hairlike grooves actually can be traced across the *museau* running at right angles to the curve of the lips (see fig. 4A). We believe these grooves to be an adaptation allowing uniform disbursement of the tiny volumes of air that occupy the sacs during deep dives—a point we will return to later.

The lips of the *museau du singe* empty into the distal sac, a roughly triangular flaccid black-walled air space swinging off to the right as one explores dorsally from the *museau*. The sac effectively covers the entire anterior end of the spermaceti organ.

At the left corner of the *museau* a passage, the *connecting sac*, connects the distal sac with the vestibule, a small space lying just below the S-shaped blowhole and thence connecting into the left nasal passage. The otherwise black anterior wall of the distal sac bears a white horizontal ridge of stiff connective tissue, which fits precisely into the anterior line of the *museau* lips (fig. 5).

The left nasal passage passes posteriorly from the blowhole along the lateral surface of the spermaceti case as an elongated pipe-like tube whose thick opposite walls interlock with one another in a roughly S-shaped cross section. This shape seems to be an effective way to allow complete closure (as would be necessary under high hydrostatic pressure) and also to permit rapid and wide opening without stretching the tissues. Surrounding the entire tube are circular muscles that seem capable of exerting constrictive pressure on the narial canal. This passage then dips ventrally into the very large and asymmetrically placed left naris, which is also occluded by a muscular mass.

It seems likely that the large direct connection of the left naris is used during rapid expiration and inspiration of the "blow" and is thus the respiratory pathway capable of handling large volumes of air very rapidly, while we speculate that the much smaller and more complicated right passage, interrupted by the *museau* and broken into sacs in two places, is concerned with phonation and that both passages are linked to-

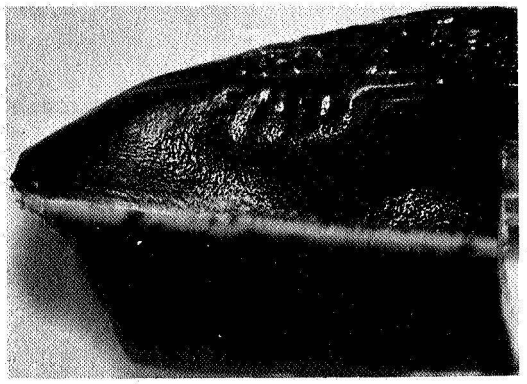

FIGURE 5. Triangular ridge of the anterior wall of the distal sac, which in life fits tightly into the indented line of the museau lips.

gether, thus allowing recycling of the air used in phonation.

Museau du Singe

At the anterior end of the right nasal passage, emptying into the distal sac, are the remarkable lips mentioned earlier. They occupy the entire width of the distal sac. The lips remain tightly pressed together even after dissecting away the stout overlying connective tissue. One can force a hand between them, but the pressure is sufficient that circulation would be cut off if the hand were left inside for long. This pressure apparently results not from muscle tension but simply from the dense connective tissue structure of the lips and surrounding snout. When the lips are pulled apart, one can see bands of very hard, almost horny whitish cornified tissue running in a perfect arc on the inner labial surfaces (fig. 2b). Closer inspection shows that each such band is composed of three concentric flattened ridges with two flat-bottomed grooves between. The upper and lower lips mortice together when closed almost as if machined.

Lying anterior to this band, both above and below, the borders of the lips fall away in a band of rather stiff crenulated folded black tissue. It is interesting that the pygmy sperm whales (*Kogia* sp.) possess similar lips and morticed borders, but they are located within the skull amphitheatre posterior to the small spermaceti organ. The same is true of a single Hyperoodontid whale that we examined in this regard, a Cuvier's Beaked Whale (*Ziphius cavirostris*) taken on Oahu, Hawaii, and examined by the senior author. In it a small subcylindrical fatty organ, that may be homologous to the spermaceti organ, occupied an excavation in the surface of the rostrum and communicated posteriorly to the right nasal plug that was lined on its surface by a mortice-bordered *museau*. We feel that the presence of this remarkable structure in these different groups of whales indicates a community of ancestry which, however, must be fairly ancient since the groups were clearly defined in Miocene time (ref. 5).

The upper lip of the *museau* gives way to a hemispherical dome whose surface forms the posterior wall of the distal sac. The connective tissue overlying the outer wall of the distal sac and the lower lip of the *museau* is extremely thick and very dense reaching a thickness of more than 15 cm in an 11-m whale.

Frontal Sac

It is our contention that the frontal sac, which lies adhered to the face of the skull amphitheatre, is the posterior member of a pair of sound mirrors bounding the ends of the spermaceti organ. We further suggest that its posterior wall serves to preserve the integrity of this mirror during the prodigious dives of sperm whales and during any body orientation (fig. 6A). To examine these ideas we must look at the detailed anatomy of both walls. The posterior wall of the sac is covered with a pavement of smooth, rounded, fluid-filled knobs and overlies the skull amphitheatre. The knobs vary in diameter from 4 to 13 mm with a mean diameter of about 9 mm. Each is formed of tough walls of collagenous fibers and is filled with serous fluid. Between the knobs lie grooves varying from 3 to 12 mm deep. Scattered throughout these channels are thin membranous transverse septa that divide the channels into many discrete parts, each part consisting of a small ramifying set of passages (fig. 6B). The anterior sac wall is dramatically different from the posterior wall, being a smooth compliant surface.

As the whale dives, external pressure must

FIGURE 6a. Frontal sac of an 11-m sperm whale. The man's hands grasp the dorsal ridge of the skull amphitheatre and touch the posterior wall of the frontal sac (a) that lies adherent to it. Note pavement of fluid-filled knobs. Reflected forward is the posterior wall of the spermaceti organ (b) which forms the anterior wall of the sac. Organ has been emptied of spermaceti and the wall, which is normally vertical and conforming to the contour of the knob-covered posterior wall, lies "deflated."

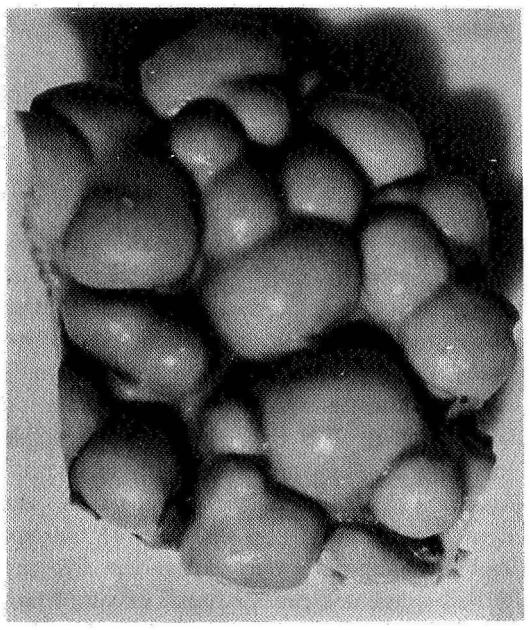

FIGURE 6b. Detailed view of knobby posterior wall of frontal sac. Note membranous separations at (a).

keep these two walls pressed against each other most of the time. Only when the animal exerts muscular pressure upon the air contained in its respiratory system can the walls be expected to part. As the animal reaches great depths, the available air volume will become so small that it would not be possible to part the walls more than millimeters at most, if at all. For instance, sperm whales have been recorded swimming at 2250-m depth (Whitney, William, *in litt.*), where air volume in the respiratory tracts will be reduced to 1/250 the surface volume. At such a depth the only air space possible would be deep between the knobs.

Because the knobs of the posterior wall are fluid filled, they are deformable but incompressible (fig. 7). As the soft anterior wall presses over them, it must conform part way into the channels between knobs, restricting air to these channels. The seal thus produced, in combination with the septa, will lock a filigree of air between the knobs within a series of small areas defined by the septa. In effect, a filigree of air films set on edge with regard to the spermaceti organ will result and will be maintained regardless of the body orientation of the animal. The fluid-filled knobs, wherever they remain uncovered by an air film, will partially transmit incident sound in a relation between knob diameter and wavelength, while the filigree will reflect. Even an air film a fraction of a millimeter thick is essentially a perfect sound reflector (ref. 6). The result should be that any sound hitting the sac wall from the spermaceti organ should be partly reflected completely by the air filigree and partly filtered and passed posteriorly through the knobs in relation to their dimensions and the frequency

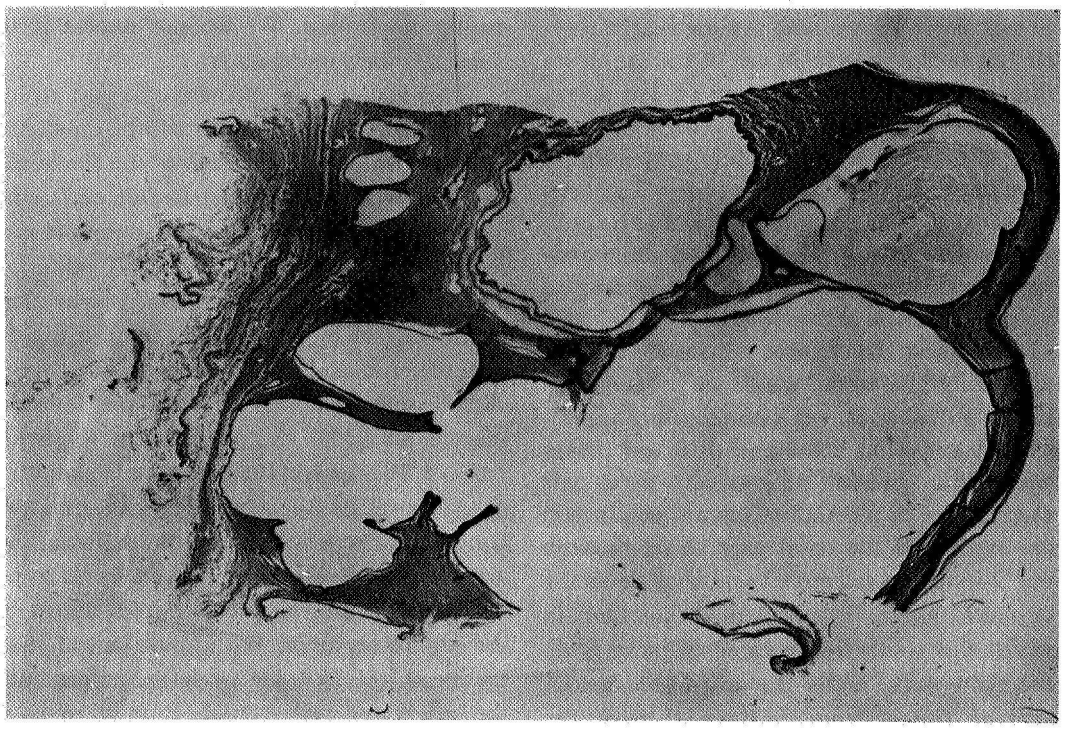

FIGURE 7. Section through the knobs of the posterior wall of the frontal sac showing their hollow nature and fibrous structure.

composition of the incident sound. This effect may be expected to vary with the depth of dive as the available air volume varies, and hence the coverage of the knobs by an air film varies in completeness.

Air Recycling

Sperm whales routinely dive for an hour, or perhaps more (ref. 7). Those who have listened to sperm whales uniformly report continuous click production from them, including records from animals deep beneath the surface (ref. 8). Our own encounters tend to confirm this view. Thus, if air is used in sperm whale click production, it must be recycled since its total volume is relatively low and completely insufficient for continued sound production (over such long periods) if used only once.

Those odontocetes that have been observed while phonating under water do so largely without release of air. Occasionally a stream of bubbles will accompany a sound emission, usually a whistle in porpoises, but much more commonly, none is released at all. Close inspection of such phonating animals shows movements of the blowhole valve and complex swellings over the superior nasal sacs at the time of phonation, suggesting the use of air in sound production. It is known that air pressure levels inside the air sac system may be considerably higher than ambient pressure (ref. 9).

Thus, if the sperm whale phonates generally in the way the delphinid porpoises men-

tioned above do, we may assume that it recycles air in the process. Much of the sac structure and other soft anatomy of the sperm whale forehead bears a phylogenetic relationship to that found in delphinid porpoises, although one rather ancient in time (Oligocene or older), so this contention is probable. Both groups possess complex sacs and nasal passages; both have paired passageways deep to a single blowhole and so forth.

Assuming that sperm whales do recycle air during phonation, which we believe to be highly probable, how is such recycling accomplished and what is the path it takes? Three possibilities present themselves. First, air might move in a complete circuit, coming up one naris past the nasal plug valve, through the U-shaped canal circuit and back down the opposite naris. The obvious direction in which this would be expected to move is up the right naris, under the spermaceti organ, through the *museau du singe*, through the distal sac, through the connecting sac, the vestibule, and back down the left narial passage to the left bony naris. It seems unlikely that it could move in the opposite direction since such movement would be against the *museau*, which, since it is not actuated by muscles, would seem to be opened only by air pressure from behind, acting in the manner of a stop-check valve.

The second possibility is that air might move back and forth in the loop of canals and sacs. This seems unlikely, once again because the *museau* appears incapable of being opened except by pressure from behind. Thus we infer that air cycles through the circuit starting at the right naris and returning into the left naris. The third possibility is that it might move up both passages simultaneously, but it seems obvious that this could only happen with the blowhole open, as is the case during respiration. We do not expect it to occur routinely underwater.

This leads to the question: "What structure pumps the air?" If air returns down the left naris from the sac system of the forehead, the first junction between the left and right naris occurs just dorsal to the arytenoid extension of the larynx where the posterior bony nares enter a common bony excavation at the base of the skull. The larynx is highly muscularized and might function as a recycling pump equipped as it is for forward movements within the nasopalatine sphincter (see ref. 10), or what seems more likely to us, pumping might be accomplished within the bony nares themselves. As in the *museau*, the arytenoid extension of the larynx seems to be a valve opened by air pressure from deeper in the respiratory tract. We suspect its spoutlike tip limits recycled air from excursions into the larynx and deeper, perhaps in all odontocetes, and that air thus simply moves down the left bony naris, enters, and is pumped within the right naris during recycling. A pumping mechanism within the bony naris seems the most likely location, since a positive pressure could probably best be developed by the action of muscles on an airway over a substrate of rigid bone, rather than against soft tissue. Within each naris is an elongate muscle mass, the pterygopharyngeus muscle, that seems capable of occluding the passage when contracted, and when relaxed, to open it again. Lawrence and Schevill (ref. 10) describe it as follows: "Its origin is from the anterior wall of the upper part of each bony naris." This arrangement could conceivably function in a manner of a peristaltic pump. We can bring no evidence to bear which tends to resolve which structure, if either, might be involved.

SPERMACETI AND OTHER ODONTOCETE OILS

Spermaceti is a complex waxy oil, liquid in the living whale. Its density is 0.782 gm/cm^3 at 60° C. K. J. Diercks of the Defense Research Laboratory, University of Texas, kindly determined the sound transmission velocity in spermaceti as a function of frequency (table 1).

Within the range of frequencies tested, spermaceti is nearly nondispersive with regard to frequency. We have been able to obtain velocity measurements on the melon oil of the hyperoodontid whale, *Ziphius cavorostris*, and a figure for melon oil of a porpoise, presumably *Tursiops truncatus*, has been cited to us by E. C. Evans (*in litt.*). Both propagate sound much more slowly than does spermaceti.

TABLE 1.—*Sound Transmission in Some Odontocete Oils*

Frequency (kHz)	Velocity (m/sec)	Temperature (°C)
Spermaceti 21	2638	36
26.77	2654	36
30	2619	36
36	2669	36
40	2684	36
Ziphius cavorostris melon pulse, broadband	1356	27.1
Porpoise (presumably *T. truncatus*)	1352.2	28.2

SPERM WHALE SOUNDS

Nearly every time one listens underwater in the vicinity of sperm whales, one hears a monotonous series of clicks (ref. 8). These clicks are sometimes very intense; measurements range from 73.9 dB re. 1 dyne/cm^2 to 75 to 100 dB re. 1 dyne/cm^2, both presumably at 1.0 meter (Whitney William, *in litt.*, ref. 11). Sperm whale clicks may carry for a matter of miles underwater. Most delphinid clicks, by contrast, cannot be heard as much as 1000 m. Although some workers have reported single clicks in sperm whales (ref. 12), all the sperm whale signals we have examined could be resolved into a burst-pulsed structure. Claims to the contrary seem to be based upon different nomenclature rather than a basic variation in signal structure since Busnel and Dziedzic figure a sound spectrogram showing a burst pulsed character within a signal they consider to be a single burst. These burst pulses consists of six to eight complex transients, each 0.5 to 1 msec in length, rapidly damped from the initial high intensity signal into background level. The entire click is usually close to 25 msec in length.

In the many hours of listening to sperm whales by several investigators, two have reported signals other than clicks (refs. 12 and 13). These signals, which were rare in the records of these two investigation teams, consisted of squeals recorded in the vicinity of a sperm whale pod. Their rarity requires that their production by sperm whales must still be considered insecure.

Typically, sperm whales emit trains of clicks given at repetition rates up to 60 to 80 per sec. Such trains may sometimes be quite prolonged, continuing for a minute or more. The highest repetition rates occur when a sperm whale is apparently examining a nearby object, as when a phonating whale swam over to and hit our hydrophone. It is interesting to correlate the click rates of delphinids such as *Tursiops truncatus* during such behavior (400 to 500 sec, see ref. 14) with these rapid rates of the sperm whale. Since the burst pulsed clicks of the sperm whale each consists of six to eight pulses, while delphinid signals consists of single transients, we can calculate that each animal is emitting between 400 and 500 brief pulses of sound/second when it is engaged in close-up inspection.

Within the cacophony of clicks coming from a pod of sperm whales, one can discriminate trains from individuals. Typically the

repetition pattern will allow one to inspect the entire train (fig. 8). What emerges is that some features of the click train are constant while others vary. Among the constant items is a "signature" that can be discerned in the structure of the individual pulses that make up each burst pulse. This appears to be typical of each individual whale. The spacing of pulses within the burst pulses of such a click train is quite constant, although some of our recordings show some pulses at irregular intervals that we cannot be sure do not represent another more distant animal or variability from some other source. One may lay a multipoint proportional divider over the burst-pulse clicks of a single animal and find uniformity throughout a long click train. The spacing of pulses (interpulse interval) varies from animal to animal, and we assume this variation is due to different lengths of spermaceti organs. Interpulse intervals range from 2 to 4.8 msec (ref. 8).

On the other hand intensities, frequency composition, presence of minor transients, and duration of individual pulses change sequentially as one inspects the clicks of a long train. We take these variations to be due largely to the changing headings relative to the recording hydrophone taken by the animal as it swims through the water. The constant features of the signals we take to be due to regularities in the geometry of the generating and transmitting structures of the whale and in its mode of sound production. We suggest that the regular spacing of pulses within a burst pulse represents reverberations of a single signal within the spermaceti organ.

We propose that a single intense click is emitted at one end of this organ and that the first pulse probably represents this initial signal transmitted directly into the water ahead of the whale, while the remaining pulses represent reverberations of the backwardly directed portion of this signal between the two air mirrors that bound the ends of the spermaceti organ. Obviously there are several unanswered questions here that need to be explained. Where are the clicks produced? How do they leave the spermaceti organ?

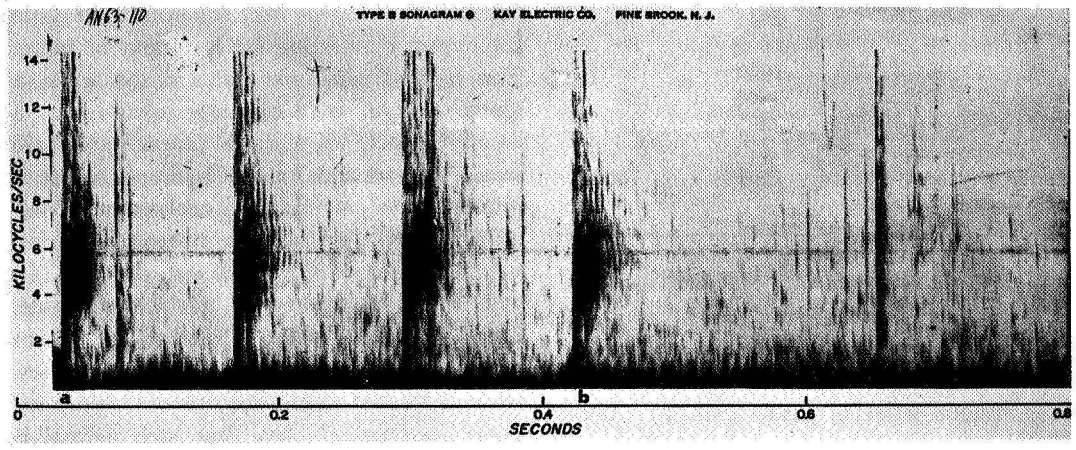

FIGURE 8. Sperm whale burst pulse clicks showing broad band character of first pulses of the click (a) and subsequent narrowing of the band as the burst pulse is damped (b). Courtesy William Schevill, the horizontal stripe near 6 kHz is an artifact. Filter bandwidth is 600 Hz.

Are the geometry and dimensions of the spermaceti organ such that this explanation could be true?

First let us look at the dimensions and geometry of the spermaceti organ in relation to emitted signals. Since we know the speed of sound in spermaceti, and we know the lengths of spermaceti organs relative to the total length of sperm whales, it is a simple matter to calculate the spacing we would expect to occur between pulses of a burst pulse, if they represent reverberations. As sperm whales grow older, relative length of the spermaceti organ appears to increase somewhat as the spermaceti organ more and more overhangs the upper jaw (ref. 2). However, for our purposes, a figure varying from about 25 to 40 percent of the total length of young adult animals appears correct.

If our theory is correct, the regular spacing between pulses represents two traverses down the length of the spermaceti organ between the bounding sound mirrors. This must be true wherever the initial sound is produced relative to the spermaceti organ. Thus we can calculate:

$$\text{Length, spermaceti organ (meters)} = \frac{0.5\ (\text{interpulse interval})\ (\text{sec})}{\text{speed of sound in spermaceti organ}\ (\text{m/sec})}$$

To test our theory we need sounds recorded from an animal of known dimensions; a difficult bit of data to obtain from a live sperm whale at sea. However, an unusual opportunity came our way while recording underwater sounds 29 km off Mejillones in northern Chilean waters on August 16, 1968. On a very calm day a single sperm whale was sighted while the recording team was cruising the coast in a 9-m felucca (a local double-ended fishing vessel). The animal approached the vessel, emitting a constant train of sounds, swam directly alongside, and actually hit the hydrophone with its head before the crew panicked and raced away. The recording crew was able to make an estimate by eye of its length relative to that of the boat as it surfaced alongside the vessel. They estimated it to be as long as the boat or about 9 m.

Regarding the length of the spermaceti organ compared to body length in this animal, we refer to Nishiwaki, Ohsumi and Maeda (ref. 2) who list the length of the severed head in a 9-m whale as about 29 percent of body length, or 2.6 m.

When the signals recorded from this single animal were analyzed, they were found to have an interpulse interval of 2 msec, and when this is converted to spermaceti organ length (2.65 m), a predicted animal length of 9.18 m is obtained; a remarkable correspondence with the observed length (fig. 9). The longest interpulse intervals which have been recorded from sperm whales (4.8 msec.) would have come from animals about 16 m long, according to our predictions.

Other questions remain unanswered: If the air sacs that bound the spermaceti organ are sound mirrors, how does sound escape after traversing the organ to produce the component parts of the burst pulse? We suggest that the distal mirror at the anterior end of the organ may be functionally incomplete and may allow sound emission over part of its area while maintaining its reflective integrity elsewhere. The exact exit site suggested is the upper lip of the *museau du singe*, where the ridge of the anterior sac wall must normally lie tightly pressed against and between the lips (see fig. 3). Further the spermaceti organ terminates anteriorly in the upper lip of the *museau* as a broad wedge invading the tissue of the lip, and thus a direct channel for sound may be present. Rigid heavily crenu-

lated tissue lines the lips both above and below the *museau* and must serve to prevent tight contact of the spermaceti organ and anterior sac walls in these areas thus maintaining a partial mirror.

An alternative exists. It is possible that sound exits through the well developed mesorostral cartilage of the upper jaw and that sound is somehow piped into this structure from the rear after being reverberated back and forth in the spermaceti organ. Because of the circuitous course sound would have to follow, we consider this possibility more unlikely. Once again, measurements from a captive emitting whale are needed.

If the sound generator was located some distance away from the spermaceti organ, the interpulse interval between the first and second pulses of a burst pulse should reflect this be being either longer or shorter than that between the remaining pulses that should be evenly spaced. In general, pulses within a burst-pulsed click appear to be equidistant, so we conclude that the sound generator is either very close to an end of the spermaceti organ or actually located there. This pinpoints two structures as possible sound generators: the *museau du singe* located at the anterior end of the organ and the right nasal valve located above the right superior bony naris. The *museau* is, of course, in proper position, while the right nasal valve is located some distance anterior to the posterior end of the spermaceti organ and directly under it. Measurements of the skull of a 13-m animal show that approximately 10 percent of the total length of the spermaceti organ lies posterior to the entry of the right bony naris on the superior surface of the skull. If sounds are produced in this location, a signal with complex spacing of pulses should result. The

FIGURE 9. Sperm whale burst-pulsed click recorded from 9-m whale swimming alongside 9-m felucca, 29 km off Mejillones, Chile, August 16, 1968. 2 msec/cm sweep, 0.2 volt/cm amplitude. Recording by Leanne Hinton.

part of the pulse that is propagated forward would arrive in a straight path to be followed by reverberations from within the spermaceti organ following in such a fashion that the first interspace between pulses would be slightly more than half the interval between subsequent pulses. At the same time, reflections from this signal, which were propagated posteriorly at the moment of emission, would be superimposed on the other parts of the signal. A complicated signal would result in which the interspaces between the pulses are far from uniform. Because the burst pulses of sperm whales show regularity, we feel, therefore, that it is unlikely that sounds are produced at the right nasal plug. Once again the *museau* seems the most likely locus.

How then could sounds be produced by the *museau*? We have no direct data to present on such sound productions but can infer the following from the anatomical arrangements we see. First the *museau* being a one-way or stop-check valve suggests that it is opened and closed by air pressure from behind. Thus we suggest that it is actuated by air pressure built up from below the superior

bony naris and that this pressure forces air along the groove system previously described against the back of the *museau*. The air pressure at some point can be expected to overcome the connective tissue tension which normally keeps the lips closed. At this point the lips might open and slap back together again producing an initial pulse.

It is quite possible that this is a gross oversimplification of this proposed sound production mechanism. We are intrigued by the extensions of the groove system over the *museau* lips. These narrow very markedly as they pass across the morticed border of the *museau*. We wonder if it is possible that as the lips are forced apart by air pressure and return to their normal closed position, if a Bernouilli effect might be produced in which the velocity of air passing forward across the lips is speeded past the speed of sound and produces a tiny "sonic" boom, somewhat in the manner of the production of sound by snapping shrimp. The high intensity of sperm whale clicks suggests that more than a simple clapping together of the lips may be involved in the sound production.

SPERM WHALE MODELS

If our theory about sound production in the sperm whale is approximately correct, it should be possible to simulate the sound production apparatus in the laboratory and to see if we could thus produce signals like those recorded from sperm whales. Our attempt was to take the structural characteristics we found in the sperm whale and to use these directly in the construction of the model. The criteria we used were these:

(1) Dimensions of spermaceti organs

(2) Position and completeness of the sound mirrors located at either end of the organ

(3) Speed of sound in cetacean head oil (since our models were constructed in air, these velocities were corrected for the velocity difference between air and spermaceti)

(4) Simple broad band impulsive nature of the initial click of a sperm whale burst pulse, which is considered to represent the initial sound emission.

Three models were constructed. The first consisted of a vinyl pipe 20.6 cm in diameter and 85.5 cm long with one end closed by a solid vinyl plug and the other partly closed by a solid vinyl plug having a 7.6-cm diameter hole in the center. This chamber was excited by a 7.6-cm loud speaker that was driven by the arrangement shown in figure 10. The loud speaker was located near the opening in the chamber. A simple 1.2-msec pulse was used to excite the chamber. This excited the longitudinal mode of the chamber

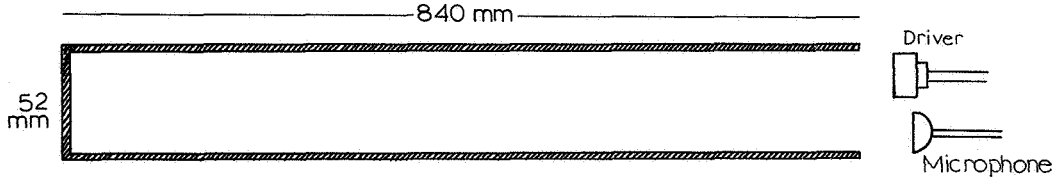

FIGURE 10. Artificial sperm whale. A single 200-μsec pulse was used to drive the chamber, which was constructed of PVC pipe and filled with air.

as well as other modes because of reflections from the walls. From this single pulse there was generated a train of gradually decaying pulses that contained 20 or more distinct pulses. The signal envelope very much resembled those of *Physeter* clicks. The successive reflections were 4.6 msec apart compared to the pulse spacings published for *Physeter* which were 2.0 to 4.8 msec apart and contained five or six distinct pulses. Obviously the natural click was much more rapidly damped than this initial artificial click. The second model consisted of a 200-cm vinyl pipe with one end closed with a solid vinyl plug and the other open. The same electrical system was used except that a miniature driver unit from a military headphone (type D3T, 50-ohm impedance) was used to excite the column. By using a simple single pulse 200 misec long, a train was generated that more closely resembled a train of *Physeter* clicks (fig. 11). There was slightly more damping within the successive pulses.

The third arrangement was identical to that in no. 2 except that the pipe length was reduced to 100 cm. The oscillator was set to 2060 Hz so that it passed approximately two cycles. These values were chosen to produce a train as nearly like that as *Physeter* as possible. Several things of interest were noted during these tests. First, by adjusting the rate at which signals were introduced into the column, we could produce very great changes in the intensity of emitted sounds presumably by reinforcements within the column. Second, the size of the speaker used to introduce sounds to the column greatly changed the stability of the emitted signal. A speaker nearly the width of the column was capable of producing very stable sounds while a smaller one was less capable. This is suggestive, once again, that the *museau* is the site of sound production since it represents a pair

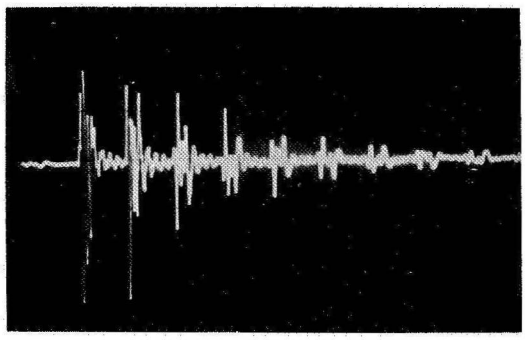

FIGURE 11. Artificial sperm whale burst-pulsed click produced by the 52 × 840 mm acoustic model. Amplitude 0.1 volt/cm. Sweep 5 msec/cm. Note rapidly damped character of the signal and 4.8-msec separation of pulses within the click.

of lips that span the entire anterior width of the spermaceti organ and presumably it is actuated by air as a unit. The 200-cm pipe length was chosen to represent the path for sound in air that would correspond to a similar path in spermaceti in terms of transit time. The interclick interval within the pulses produced matches closely those seen in sperm whale signals.

FUNCTION OF SPERM WHALE BURST PULSES

The unique burst pulses of the sperm whale (fig. 9) are remarkably different from those of delphinid whales in that the repetition rate between burst pulses is generally much lower, reaching a maximum of 60 to 80 per second as opposed to more than 1000/sec in social cries of delphinids, and because sperm whale signals are given as clusters or bursts of rapidly damped clicks separated by long silent periods, as opposed to continuous trains of more or less constantly repeated single clicks in the case of delphinids.

Four features of the sperm whale system suggest that it may function as a long dis-

tance echolocation system for use in the open sea. First, if the sperm whale uses its burst pulsed signals for echolocating, one expects that they are used at considerable distance, probably during the dives of the animal into the deep sea. If the sperm whale operates in the same manner as has been shown for delphinids (ref. 14), in which the echo of the signal is received before another signal is emitted, then we can expect that the very slow repetition rates are related to long distance echolocation. In most cases where sperm whales have been listened to in the open sea, the repetition rates have been very slow indeed, ranging between what are best considered as individual clicks to those given at rates of less than 20 per second. Nearly all trains examined by Backus and Schevill (ref. 8) had repetition rates less than 7 per second, and thus would have allowed echoes to return in the interspace between clicks from targets 100 m or more ahead of the animal. The high rates we recorded here (60 to 80 per second) were from an animal inspecting us at very close range.

The second feature of sperm whale burst pulse clicks as echolocation signals seems optimum for long distance use in another way. A moderate amount of information can be obtained from the echo of a single click, but considerably more can be obtained from the echoes of the several pulses within a burst-pulsed click, which are given at short intervals relative to one another. Such subtleties as texture and internal composition may be better demonstrated by these compound clicks than single ones. Yet, as we have seen, long distance echolocation using single clicks in a train presents problems. The ranges may simply become too long to allow the animal to receive the echo in an interspace between pulses and still obtain the refined information that comes from analysis of many pulse-echo pairs. Burst pulses alleviate this problem in that much more complete information can be carried within a burst-pulse echo, and this information can come back in the interspace between burst pulses.

A third feature of the burst pulse that seems possibly useful to the sperm whale is that these signals allow discrimination of size whereas single clicks may not. A large squid, for example, being hit by the burst pulses of a click, will return an echo that is "mushy." The individual pulses of the click will hit the squid at many points along its length, and thus the echos of the individual pulses will merge into one another and a mushy echo will result; whereas a small target will return the pulses as discrete entities in the form of a simple echo of the original signal.

The fourth and final feature of the burst-pulse system of sperm whales, which impresses us as being related to long distance echolocation, is that the pulses of a click may very well act in the sperm whale's sound processing system in the same way that such transients would act in our own—namely through summation. The very long distances at which sperm whales likely seek their prey will involve attenuation and spreading losses of such magnitude that sperm whale clicks will reach very low levels relative to background noise in a relatively modest distance even though the initial intensity is quite high. If each of the clicks as it is received by the sperm whale causes a summation effect in the brain, the animal will be able to pick the burst pulse from background noise at a considerably reduced level compared to its ability to discriminate a single click under similar environmental circumstances. This effect was brought home with great force to one of us (Norris) by listening to the discharge of a pistol in an anechoic chamber in which a modest pop was heard and then later in an

echo chamber in which the apparent intensity of the same pistol sound was so great as to cause physical pain. The effect was produced in the first case by a single traverse of the sound across the author's receiving equipment and, in the second case, by several thousand traverses of the same sound across the ear which produced a summation effect in the hearer's brain.

SUMMARY AND CONCLUSIONS

Several lines of evidence point toward the spermaceti organ of the forehead of sperm whales as a reverberation chamber used in the production of the unique burst-pulsed signals of the sperm whale. This evidence also suggests that sounds are produced at the valvular lips of the anterior end of the spermaceti organ called the *museau du singe* and that these lips are actuated by air pressure within the right nasal passage. Structural features of the passages suggest that air is recycled from the right naris through the right nasal passages and *museau* into the left nasal passage under the blowhole and back down the left nasal passage into the left bony naris, and thence back again in a complete cycle. The suggestion is made that peristaltic-type pumps may exist within the bony nares themselves.

The structure of the two vertically oriented air sacs that bound the ends of the spermaceti organ suggest that they are sound mirrors. The posterior sac (the frontal sac) possesses a knob-covered posterior wall that is probably an adaptation allowing maintenance of the sound mirror in any body orientation and during deep dives. Finally this complex anatomical system is suggested as a device for the production of long range echolocation sounds useful to the sperm whale in its deep sea habitat, in which food must be located at considerable distances in open water.

The authors feel that these ideas must be considered as hypotheses until measurements can be taken from living sperm whales.

ACKNOWLEDGMENT

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A number of people have contributed to the development of these ideas and their partial testing. Forrest Wood III of the Naval Underseas Center, Point Loma, has several times commented that he felt the right sperm whale narial apparatus was for sound production and the left for respiration. David Bottles gave us much help with dissections and photography. V. Knudson, L. del Sasso, and S. McKay have contributed to our thinking about sperm whale acoustics, although they, of course, cannot be held accountable for what came from those discussions. William Schevill and Richard Backus have helped a great deal with discussions and data concerning sperm whales. Kenneth Bloome, Berit Bloome, and Leanne Hinton were instrumental in obtaining our recording of the sperm whale off Chile. We thank Robert Brownell for making a fetal sperm whale available to us. We also thank Thomas Dohl for his assistance at many points during this work.

APPENDIX

Since this paper has been in press, another theory for the function of the spermaceti organ has appeared in the literature (ref.

15). This theory suggests that the spermaceti organ functions to maintain neutral buoyancy in the whale both at the surface and at depth. By temperature control of the sac, the whale is postulated to rise to the surface from great depth with no physical effort. Several aspects of these ideas seem improbable to us. First a buoyancy change dependent upon the capriciously changing thermal structure of sea water will cause the whale's buoyancy relations to be altered from place to place, as, say, when it swam from gyre water having a deep and stable thermocline, like that off Hawaii, to well mixed water at current divergences. The organ could function only where the whale penetrated a thermal boundary. Over much of its range such boundaries are deep or are wholly absent where vertical mixing is strong.

The energetic values involved seem to eliminate the theory as well. The huge mass of the organ relative to the size of the whale would require great and rapid heat input to change the temperature of its spermaceti. Clarke calculates 1.6×10^4 calories to heat 1450 kg of spermaceti from 7.8° C to 33.5° C, expected figures needed to produce a small but possibly useful buoyancy change of 91.5 kg. It is proposed that this heat is provided metabolically, and the author states: "Many details of the spermaceti organ suggest that it is a heat exchanger. All the spermaceti oil is contained in minute vesicles held within a dense network of capillaries so that the circulation could heat the oil rapidly. . . ." We consider this statement incorrect and misleading. Our dissections showed the spermaceti wax to be extremely loosely held in very large vesicles. The fact that hand whalers could lower one of their number into the opened case to bail out spermaceti with a bucket gives the best perspective we know on this question. It seems inconceivable to us that the gossamer webwork of connective tissue and blood vessels that invades the spermaceti could be an efficient heat exchanger capable of repeated heating and cooling of such massive amounts of lipid tissue in short periods of time. Further, to have a buoyancy organ on one end of the body seems a grotesque arrangement. The moments produced would tend to tip the animal, in a single direction (either down or up), while what is known of underwater sperm whale tracks suggests, as one would expect, erratic searching movements (W. Whitney, *in litt.*).

Further there is no evidence that sperm whales passively float to the surface after dives. Instead normally they are obviously swimming strongly throughout them. A whale undergoing a 2500-m dive must travel about 4.8 km just to dive and return from such a depth, and when one adds a searching component, additional travel distance is required. The whale has to swim 4 knots or more just to perform such a dive in the normal hour's dive time. Passive floating seems out of the question. There are a number of other objections to the theory: blood shunting during dive cycles, as it is now known, suggests supply during dives to nervous and cardiac tissues only; the commitment of energy during growth to produce such a huge but inefficient buoyancy compensation device is suspect; buoyancy is likely much more easily controlled by other means such as lung collapse or underwater emission of air. The slight negative buoyancy encountered by a diving whale is most likely to be compensated for by a slightly greater swimming effort.

DISCUSSION

MACKAY: There is perhaps one change that should be considered in your analog, and this again brings up the matter that a sound wave shape depends on the phases of the various frequency com-

ponents, that is, sounds are not fully characterized by frequency and amplitude alone.

If you take a sound wave, e.g., a sudden compression, and reflect it off a hard wall, then it comes back as a compression. However, if you reflect the compresion from a region that is "softer" than the region in which the wave is travelling, or if the reflection is from a sudden opening in an otherwise restricted region, then the reflected wave will be a rarefaction. The reflection can be equally good in either case, and it can be considered as a matter of the phases of the frequency components. In your analog there was a loudspeaker and a hard surface, whereas the reflector in the head of the whale apparently was air surrounded by tissue. The latter probably was a more-to-less dense reflecting interface from which a sound wave would be reflected with the same amplitudes of its frequency components, but they would be inverted. A more exact analog of the whale situation might thus be the blowing of a bugle.

Do you feel that there is a single oscillation at the front end and then just reverberation, or do you feel that there are several oscillations associated with the original energy source?

NORRIS: We have not been able to be sure about phase changes in the sperm whale signals we have examined, and there may well be reversals, and they may differ from our model. The complexity in the sperm-whale pulses is greater than I have shown. We thought a high-pass filter might be involved because whenever the spermacetic organ is pressed tightly over those knobs of the frontal sac wall, sound should be transmitted back into the animal's skull. For a time I thought that the emphasized frequency present in the sperm-whale signal might be due to this, but I doubt that now. It is more likely due to the geometry of the entire whole chamber.

BULLOCK: Have you compared the baleen whales with respect to the sound production in the head of odontocetes? Why do they produce only very low frequencies rather than the high or ultrasonic frequencies of odontocetes?

NORRIS: There is an entirely different structure in terms of the nasal passages. They are absent in the mysticetes. There are differences in the larynx of the two. It may well be that the mysticytes are using their larynx while odontocetes may use other sound generation loci.

QUESTION: Would you speculate that the development of this system would probably restrict the sperm whale to the deep sea?

NORRIS: Sperm whales are, indeed, typically deep sea animals. In my experience they generally stay in water several hundred feet deep, or more.

EMLEN: A behavioral question: You also noted that there are individual characteristics for individual animals that click. Is this also a social communication signal, perhaps allowing individual recognition?

NORRIS: I would be very surprised indeed if in both the porpoises and in the sperm whale, echolocation clicks didn't have a lot of social meaning. I think almost anything an animal says has social meaning.

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SESSION V

Sensory Mechanisms—Optical Senses

Chairman, C. A. G. WIERSMA

Visual Orientation Performances of Desert Ants (*Cataglyphis bicolor*) Toward Astromenotactic Directions and Horizon Landmarks

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IN MANY ORGANISMS different systems of direction finding and position measuring are simultaneously involved in maintaining a particular orientation course. Using a whole set of direction-indicating stimuli of the physical environment, these organisms may first increase the accuracy of their orientation performances and may also be able to measure their position in space even when one part of their navigation system no longer receives information about the external directional stimuli. This presentation gives some experimental data on the visual orientation of desert ants toward astromenotactic courses and horizon landmarks involving the co-operation of different direction-finding systems.

Cataglyphis bicolor, an ant widely distributed in desert areas of northern Africa (refs. 1 and 2) and southwest Asia, is most suitable for investigations on optical orientation mechanisms, in comparison with most of the central European species:

(1) *Cataglyphis bicolor* is a predatory and solitary hunter (fig. 1), never performing mass foraging along scent trails but mainly orienting by means of visual cues.

(2) These hunting ants can be successfully trained to feeding places and will return regularly for many days when rewarded after each predatory run.

(3) The optically uniform natural environment of the desert ant enables us to present visual patterns which can be exactly defined in their stimulus properties and may not be thought to interfere with other terrestrial cues left uncontrolled.

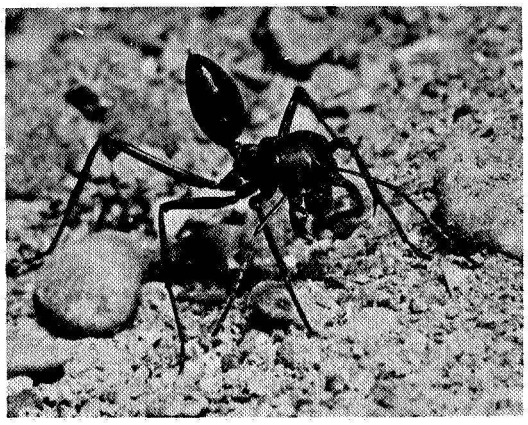

FIGURE 1. ***Cataglyphis bicolor*** **foraging with gaster placed upright in its typical position.**

Therefore, the two main demands for studying navigation systems in animals are fulfilled by training *Cataglyphis bicolor* under natural conditions: a precise presentation and measurement of the physical cues and a well established method for recording the animal's response to the orienting stimuli.

Here, I would like to deal with three aspects of the ant's visual orientation. First, it must be determined whether the ants choose a compromise direction between an astromenotactic angle and the direction toward a horizon landmark when both angles compete with each other or whether they decide alternatively between the two courses. Second this presentation refers to adaptations of the visual system to the special demands of direction finding by astromenotactic orientation or pattern recognition. Finally some data on the parameters of visual learning behavior will be presented since all the results dealt with here were obtained by using training experiments with well-defined learning parameters.

ASTROMENOTACTIC VERSUS LANDMARK ANGLES

Until recently the most extensive work on competition between an astromenotactic angle and the azimuth of a horizon landmark has been done with bees (ref. 3), followed by some preliminary experiments with ants (refs. 4 to 6). However, in all these studies performed with natural landmarks, neither the physical stimulus properties of the terrestrial cues nor the different stages of learning processes were taken into account. Up to now, the temporal aspects of spatial orientation have been ignored, as no regard has been given to the succceeding stages of one orientation course. To consider these temporal parameters, the foraging runs of the individually trained ants were exactly recorded by means of a grid of thin threads which extended over the whole experimental area (fig. 2A). To receive directional data from these graphs, a set of concentrically arranged circles was drawn around the point marking the start of the ant's orientation course. Using this procedure, one obtains a frequency distribution in angular intervals of 5°. According to statistical methods of circularly distributed data (ref. 7), a mean vector can be calculated for every distance from the start (figs. 2B and C). This vector represents the mean direction of orientation as well as, by its length, the dispersion about the mean direction.

Before we can test orientation towards celestial and terrestrial cues by means of competition experiments, we first must prove the accuracy and time compensation of the Sun-compass courses. In contrast to the circumstantial work with bees (refs. 8 to 10) and some other insects (*Orthoptera, Hemiptera, Coleoptera*), there exists only little evidence for a time-compensated Sun-compass orientation in ants (*Formica rufa, Lasius niger*: ref. 4, see also Brun (ref. 11) who failed to prove time compensation in these two species). Therefore, *Cataglyphis bicolor* was trained for 20 m to a special azimuth and then displaced in a testing grid far away from the training grid and completely unknown to the ants. There they were released and their runs recorded (fig. 3). The mean directions of the returning ants, graphed for a distance of 5 m, respectively, 10 m from the releasing point, did not show any statistically significant difference from the home direction, irrespective of whether the ants were released at once or captured in the dark for 3.5 hr before being displaced. If there was no compensation of the Sun's course during the time of capture, one would expect a deviation of 52.5°. By a special experimental procedure (which cannot be described here in detail) it was excluded that these results were influenced by

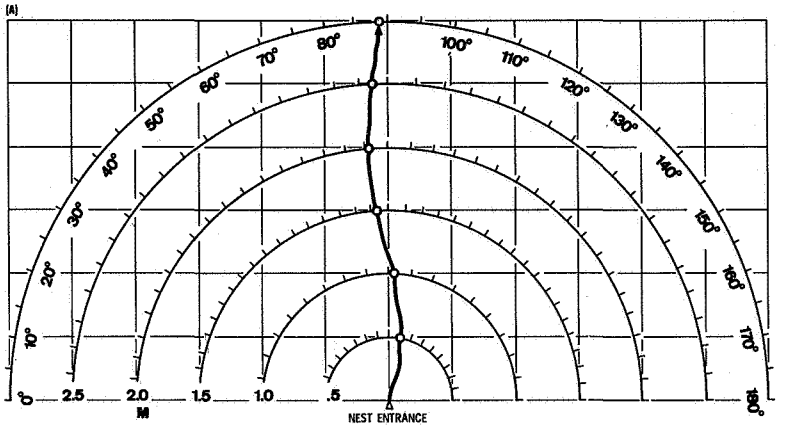

FIGURE 2. Method of recording directional data. (A) Recording of a single course by means of a rectangular grid. Concentrically arranged circles give directional information for varying distances from start of run (nest entrance).

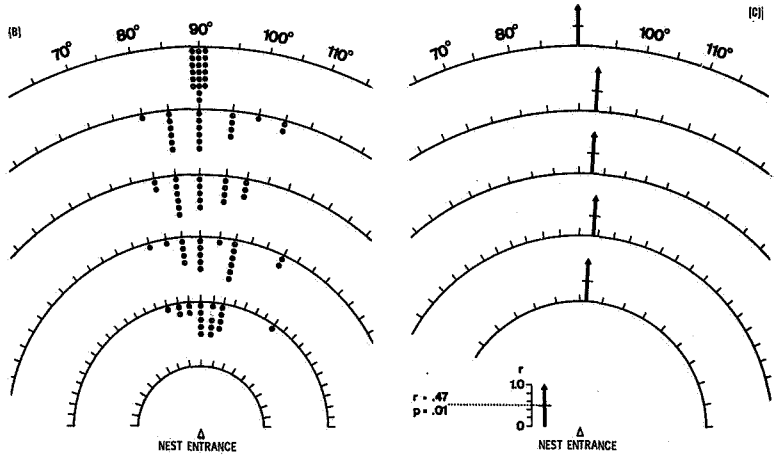

FIGURE 2 (Concluded). (B) Frequency distribution in angular intervals of 5° (n = 20 ants, training angle α = 90°, three rewards). (C) Mean vectors of frequency distributions graphed in (B). r = length of mean vector; $r > 0.47$: Preferred direction is statistically significant with $p < 0.01$.

the anemomenotactic orientation of *Cataglyphis bicolor*.

It must be added that the term "Sun-compass" orientation also includes the orientation toward the pattern of polarized light in the sky. This orientation performance can be proved before sunrise or after sunset when the ants show a bimodal distribution of directions according to the symmetrical pattern of polarized light at that time.[1] That ants are

[1] WEHNER, R.: Die Konkurrenz von Sonnenkompass- und Horizontmarken-Orientierung bei der Wüstenameise *Cataglyphis bicolor* (Hymenoptera, Formicidae). Zool. Anz. Suppl. (in press).

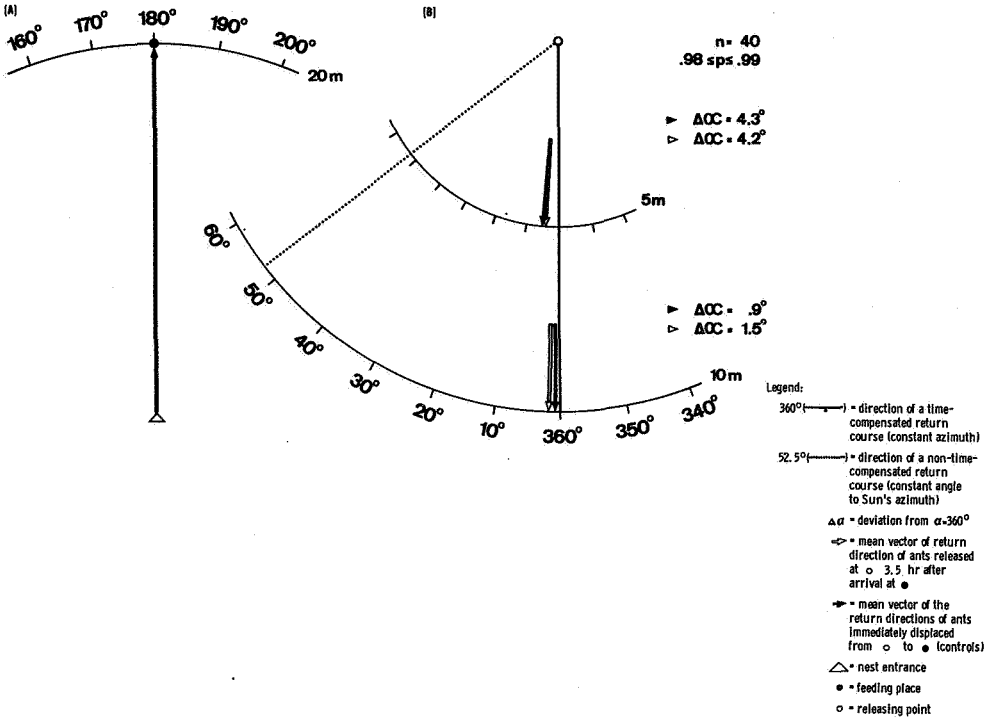

FIGURE 3. Proof of a time-compensated Sun-compass orientation. (A) Directions of foraging runs (all shifted to 180°). (B) Directions of return runs recorded in a test grid.

able to use polarized light for their orientation performances is already known for *Lasius niger* (ref. 12), *Myrmica ruginodis* (refs. 13 and 14) and *Formica rufa* (ref. 4).

In the basic competition experiment, the ants were trained to a particular Sun-compass direction, which was marked by an artificial horizon landmark consisting of a black screen having an angle size of 10° × 10°. This procedure is called "simultaneous training." After a varying number of simultaneous training runs, the position of the black screen was relocated from the trained direction by a specific amount of degrees (60° in fig. 4). The directions of the following foraging runs, indicated by the filled circles in fig. 4A, prove a clear orientation toward the astromenotactic angle. However, the ants were not rewarded until they had reached the black screen. In the following runs called "competition training" runs, the position of the black screen varied alternatively between the 0°- and 60°-direction so that the ants were always confronted with the competition situation between the direction to the horizon landmark and the Sun-compass direction of the preceding foraging run. As figures 4A and B demonstrate, the fifth run (indicated by the open squares and dotted lines) is mainly oriented towards the black screen. Furthermore, figure 4B qualitatively shows that changing from one orientation course to another does not consist of a continuous shift of a compromise direction but consists of an alternative

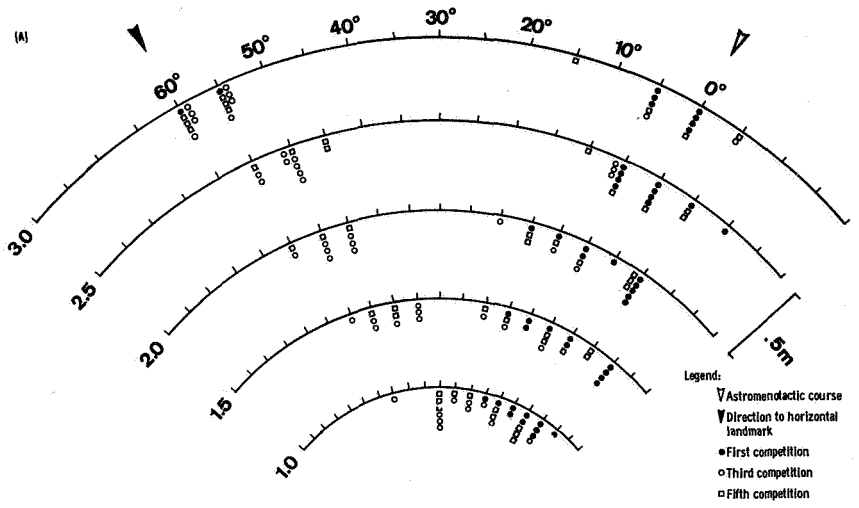

FIGURE 4. Competition between an astromenotactic course and the direction to a horizon landmark. The ants have been trained to both ($\alpha = 0°$, simultaneous training, 3 reinforcements), before the landmark is offered at 60°. See text for explanation. (A) Frequency distribution of recorded angles.

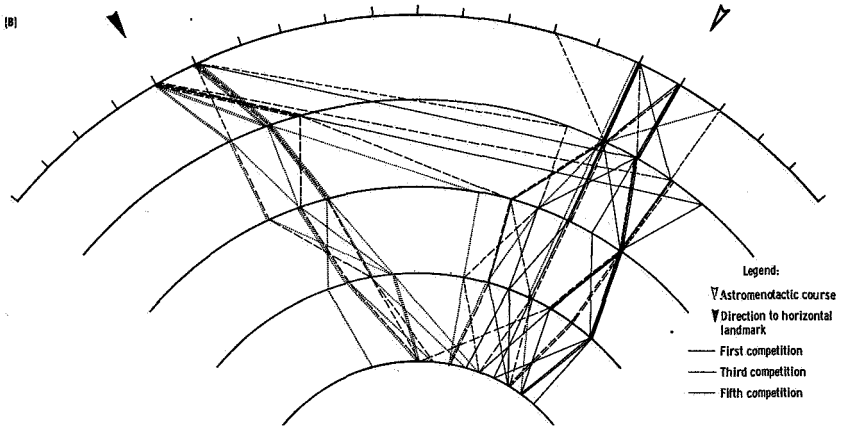

FIGURE 4 (Continued). (B) Courses of 10 individuals graphed in a generalized way.

switching over from the Sun-compass course to the terrestrial cue. The theoretically determined compromise directions, graphed in figure 4C, do not coincide with the experimental curves in figure 4B. With an increasing number of competition experiments, the point of switching over is successively relocated until it reaches the nest entrance where the foraging runs begin. This statement is proved in greater detail by figure 5. Hence, a mean vector cannot be calculated because of the bimodality of the angle distributions; angles α and β and their relations are determined for the succeeding stages of the courses:

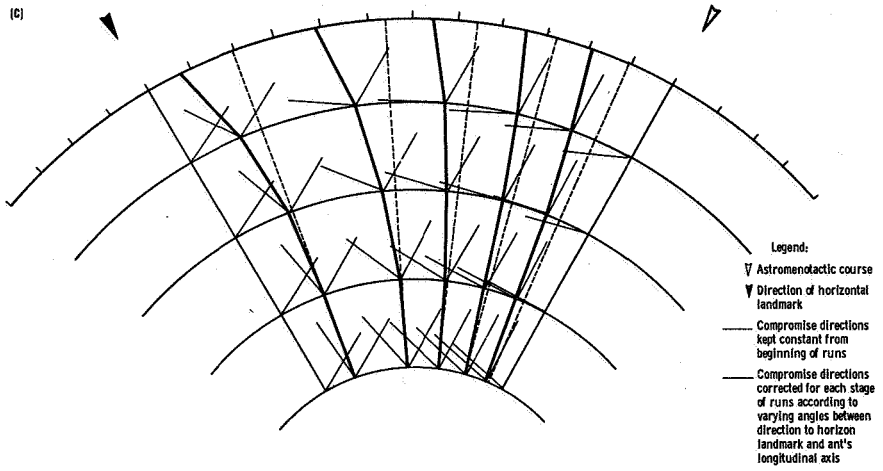

FIGURE 4 (Concluded). (C) Theoretically determined compromise directions, which do not correspond to the experimental curves in figure 4(B).

α means the deviation from the direction to the horizon landmark and β the angle included by the astromenotactic direction and the direction marked by the black screen. The relations α/β fall into two distinct groups: one about the quotient $\alpha/\beta = 1$, characterizing pure Sun-compass orientation; and the other about the quotient $\alpha/\beta = 0$, meaning orientation toward the terrestrial cue. As the lower graph (fig. 5B) shows, the proportion of the latter group relative to the first group is the larger as the distance from the nest entrance increases and as more competitive training runs are performed by the ants. Therefore, we can summarize that in the competition experiments the ants first follow the Sun-compass direction, but they can switch over to a horizon landmark by alternative decisions and not by shifting a compromise direction.

Alternative decisions are also found when the astromenotactic orientation competes: (1) with horizon landmarks in bees (*Apis mellifica*, ref. 3), where, however, the orientation courses of the flying bees could not be recorded exactly; (2) with kinaesthetic angles in spiders (*Agelena labyrinthica*, ref. 15); (3) with anemomenotactic angles in beetles (*Geotrupes sylvaticus*, ref. 16) and desert scorpions (*Androctonus spec.*, ref. 17). *Agelena* can also start in a compromise direction (refs. 15 and 18). Jander (ref. 4) also describes intermediate angles in the competition situation of terrestrial and celestial cues in *Formica rufa*. It must be noted, however, that compromise directions can be proved only when more than one of the animal's positions are recorded during one course. Otherwise an uncritically determined intermediate angle can mask succeeding alternative decisions. The hypothesis that compromise directions are built up by means of preceding alternative adjustments needs further analysis that may give more detailed information on the cooperation of the two mechanisms competing with each other.

At this points I wish to insert an additional remark on another cooperation of two direction-indicating systems in *Cataglyphis bicolor*—the cooperation of astromentactic

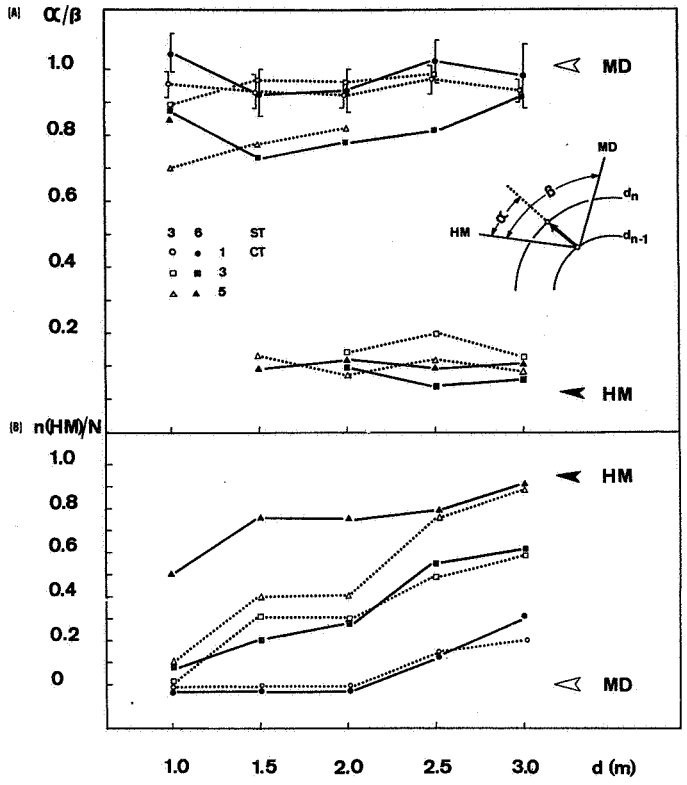

FIGURE 5. Orientation of *Cataglyphis bicolor* in competition situation between astromenotactic direction (MD) and direction to horizon landmark (HM). For explanation see figure 4 and text. Mean values are only graphed when based on at least five single values. (A) Ratio α/β in relation to different numbers of reinforcements (ST and CT) and different stages (d) of the orientation courses. α = deviation of the course from the direction to the horizon landmark (HM); β = angle between astromenotactic direction (MD) and direction to horizon landmark; ST = simultaneous training preceding competition experiments; CT = competition training to HM during competition experiments; d = distance from nest entrance. (B) Percentage of the runs directed toward horizon landmark n(HM, $\alpha/\beta \sim 0$) in relation to the total number N of runs.

and anemomenotactic orientation. Since our experiments on this subject are not yet finished, I am able to present only the main qualitative results instead of the whole quantitative data. As mentioned above, before sunrise and after sunset *Cataglyphis bicolor* orients toward the pattern of polarized light in a bimodal way by preferring the home and its counter direction. The ants were trained the previous day to an area far away from the testing grid in order to exclude all known terrestrial cues. The bimodal distribution, however, only holds for the situation when the wind is absolutely absent. When it is present and its direction coincides or—this is now important—only nearly coincides with the one during the training situation, a unimodal distribution in the right direction is obtained. However, when the wind has shifted to the counter direction, a mean vector not

statistically different from the direction 180° (home direction 0°) is due for that situation, again irrespective of the precise direction of the wind. But as soon as the Sun rises, in every case *Cataglyphis bicolor* will perform the right home direction.

From these results three main conclusions may be drawn:

(1) There exists a time-compensated Sun-compass orientation toward the pattern of polarized light because the home direction is always the counter direction of the previous training direction, notwithstanding the varying training times during the day.

(2) There does not exist a time-compensated anemomenotactic orientation although the shifts in wind direction correspond with certain hours of the day.

(3) Between the different orientation mechanisms a hierarchy can be stated as follows: The Sun-compass orientation dominates the orientation toward the pattern of polarized light, and the latter dominates the anemomenotactic orientation because varying wind directions do not result in proportionally varying home directions. The wind direction only decides which of the two courses according to the pattern of polarized light is to be taken.

Now the question may be answered: Are astromenotactic angles still recorded in an ant orienting by means of horizon landmarks, or is the mechanism of Sun-compass orientation switched off in that situation? The experiment described in figure 6 proved the former to be true. After having been trained to the two places, P_1 and P_2 which is marked by a black screen, the ants are not rewarded at the actual place of the screen (for example, P_1) but must search for the other place (for example, P_2) by means of Sun-compass orientation. If the astromenotactic mechanism had been switched off during the orientation toward the horizon landmark, the ants would follow the direction leading to P_2 as seen from the nest entrance. But, they start from P_1 in the correct direction to P_2. Therefore, an ant orienting to horizon landmarks still records the astromenotactic angle and applies that information to further navigation tasks that must be solved without the aid of landmarks. That an astromenotactic

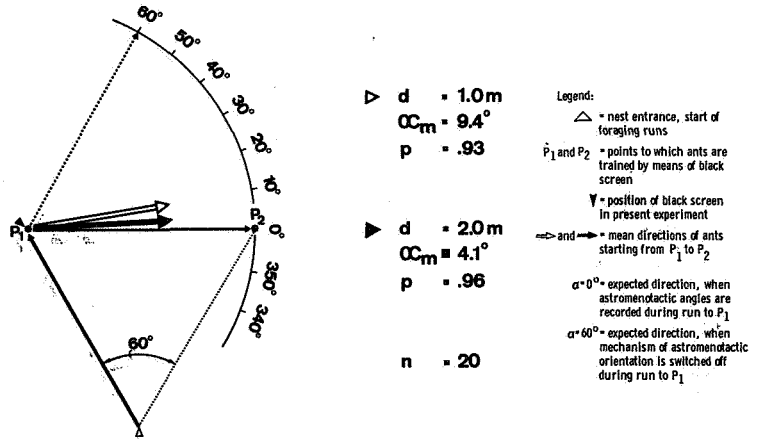

FIGURE 6. Mechanism of astromenotactic orientation is not switched off during orientation toward horizon landmarks.

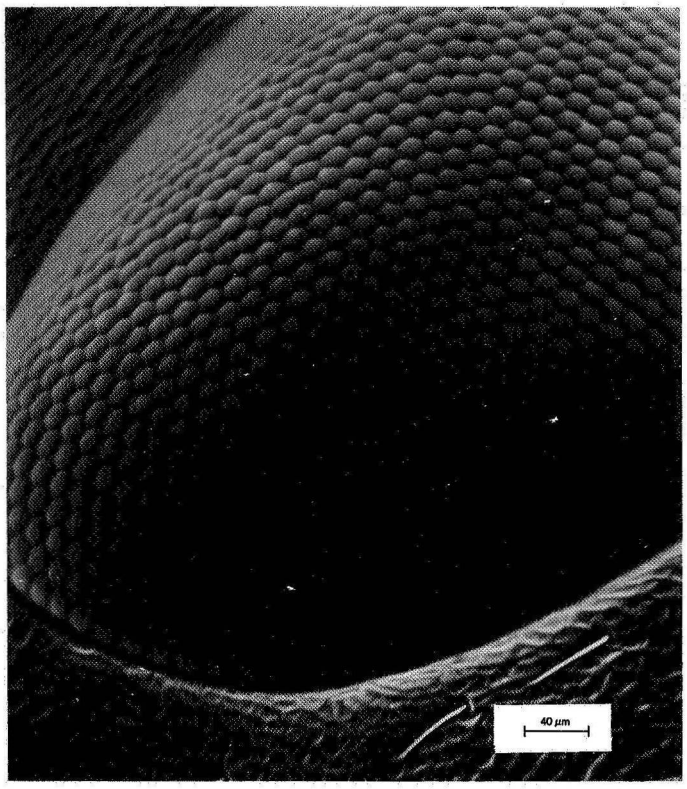

FIGURE 7. Stereoscan electron micrograph of compound eye of *Cataglyphis bicolor*. View from inside-ventral. Eye was coated by a 300 Å gold layer. Prepared and photographed by R. Wessicken, Institute of Electron Microscopy, ETH, Zurich.

course can be determined by means of other physical cues than horizon landmarks (geomenotactic angles, ref. 19; anemomenotactic angles, ref. 17) is known from *Arctosa* and *Androctonus* (Arachnida).

VISUAL CUE ADAPTATIONS

Adaptations of the visual system on astromenotactic orientation and pattern recognition are now discussed. Since we have now proven two mechanisms of visual orientation which are not linked together by building up a compromise direction, one may ask whether the visual system has developed special adaptations supporting one or the other mechanism. Let us first look at some topological relations within the visual field. By scanning electron microscopy (figs. 7 and 8) one can study receptor properties of the ant's compound eye, for example, radius of curvature and diameter of the corneal facets. When these and other parameters are measured for different size classes of the ants and different regions of the compound eye, highly significant differences can be found (fig. 9). Proceeding from the ventral to the dorsal parts of the eye, the diameter of the corneal facets decreases whereas the radius of curvature increases. Both parameters are shown for three size classes of ants with proportionally varying numbers of ommatidia.[2] They prove

[2] MENZEL, R.; AND WEHNER, R.: Augenstrukturen bei verschieden grossen Arbeiterinnen von *Cataglyphis bicolor* (Formicidae, Hymenoptera). Z. vergl. Physiol. (in press).

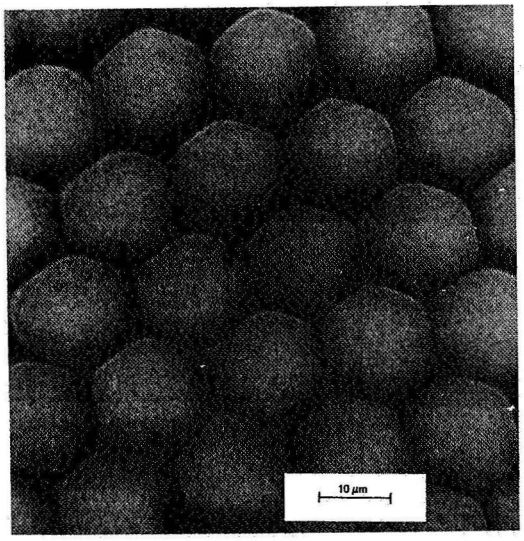

FIGURE 8. Corneal facets from ventral-external region in compound eye of *Cataglyphis bicolor*. Stereoscan electron micrograph by R. Wessicken, Institute of Electron Microscopy, ETH, Zurich.

that the interommatidial inclinations become the smaller, the more dorsal the ommatidia are situated (for bees see ref. 20). The smallest values are obtained in the internal quarter of the dorsal half of the eye where, even morphologically, a small depression can be seen looking straight upward to the sky.

Until now we have not proved whether, in desert ants, there are also adaptations of the visual system to the orientation by terrestrial cues. But our work dealing with the mechanism of pattern recognition in bees gives clear evidence that this is the case. By means of an apparatus (ref. 21) we are able to train bees to screens with black and white areas in different positions of the visual field. When the bees are trained to disks—the upper and lower halves of which are black and white, respectively (fig. 10)—the disks are chosen to a lesser degree when contrasting areas are inserted into the lower rather than into the upper part of the visual field. The reaction frequencies of the bees to the four test patterns are related to the reaction frequency 1 of the actual training pattern. The smaller the reaction frequencies are, the more effective is the insertion of the contrasting area into the training pattern. These results lead to the conclusion that distributions of black and white areas are most precisely analyzed in the lower part of the frontal visual field upon which horizon landmarks are normally projected. As known from electrophysiological recordings, single units in the optic lobes of crustaceans (ref. 22) and flies (ref. 23) have their receptive fields in special parts of the whole visual field of the eye.

That special parts within the visual fields of arthropods are due to certain orientation performances is also known for optomotor responses (*Uca pugnax*, ref. 24), telotactic orientation toward single light sources (several insect species, ref. 25), and prey catching (*Stagmatoptera biocellata*, refs. 26 to 28). Color receptors are also disproportionally distributed over the compound eye (*Periplaneta americana*, ref. 29; *Libellula quadrimaculata*, ref. 30; *Notonecta glauca*, refs. 31 and 32; *Ascalaphus macaronius*, ref. 33; *Apis mellifica*, ref. 34). Therefore, the visual system of insects may be topologically subdivided according to the demands of the different optical orientation mechanisms.

LEARNING PARAMETERS

Finally we must consider some central processes involved in the two mechanisms of visual orientation. However, only a few remarks can be made in this presentation concerning the visual learning capacities of *Cataglyphis bicolor*. First the question arises, whether the Sun-compass direction to a special feeding place is learned during the preceding return or foraging runs. Figure 11 shows the latter is true. In this experimental

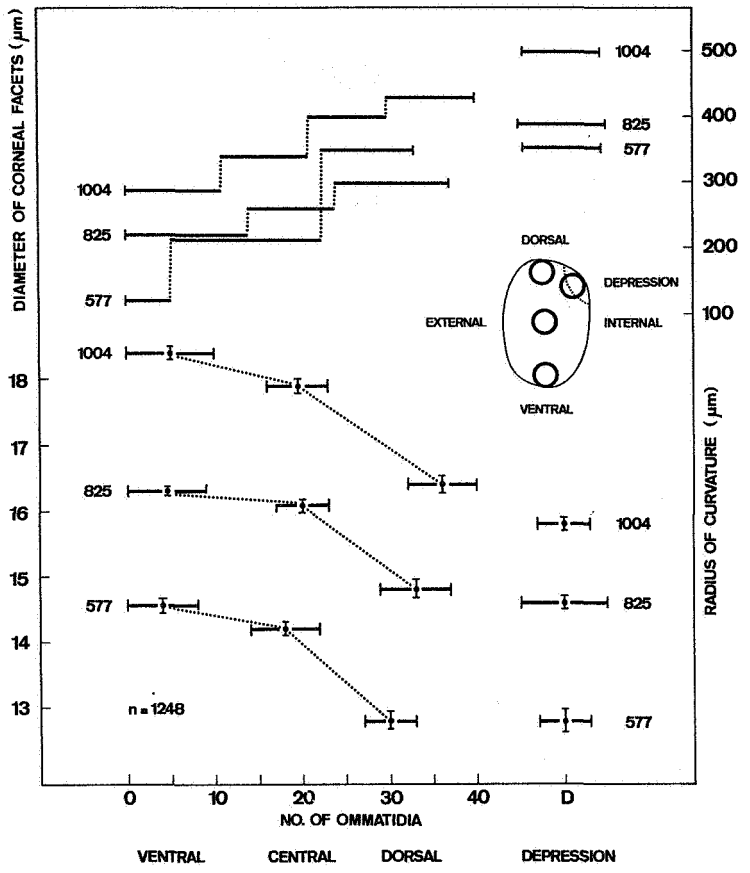

FIGURE 9. Radius of curvature (upper graph) and diameter of corneal facets (lower graph) of compound eye of *Cataglyphis bicolor* as taken from stereoscan electronic micrographs. Values are determined for small, medium and large individuum and for four regions of the eye (see inset figure). Body size (lateral length of head 1.0, 1.5 and 2.0 mm) and number of ommatidia (577, 825 and 1004) are positively correlated. In lower part, mean errors of mean values are graphed. Number beside each set of data represents total number of ommatidia in the eye.

setup the ants were trained to a feeding place and displaced to a nearby releasing point. The mean vectors of the first stages of the return runs are indicated by the black arrows. Afterward, the ants returned to the nest entrance. When measuring the directions of the following foraging runs (marked by the white arrows), one finds these directions to coincide with the Sun-compass course of the preceding foraging runs but not with the mean direction of the preceding return runs. Therefore, no learning of a new compass direction occurs when the ants return to the nest after being rewarded (refs. 10 and 35).

This conclusion is confirmed by another more direct experiment in which an astromenotactic course competes with the direction toward a horizon landmark during the return run. In order to obtain that test situation, *Cataglyphis bicolor* was trained in a

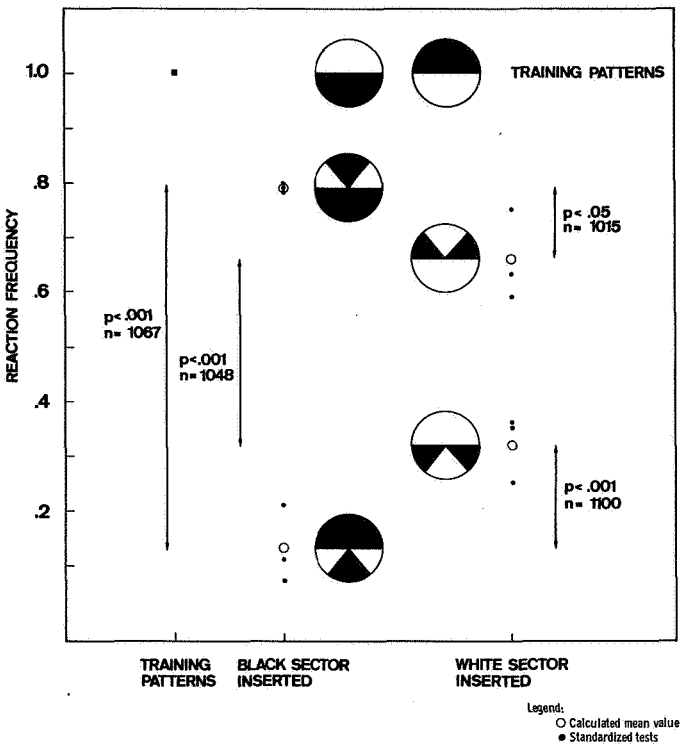

FIGURE 10. Dorsoventral asymmetry in visual field of honey bee (*Apis mellifica*). Reaction frequencies of trained bees to four test patterns (diameter 130°) are related to reaction frequency 1 to actual training pattern. Smaller reaction frequencies are more effective in insertion of contrasting area in training pattern. Each mean value is calculated from reaction frequencies of three standardized tests.

particular Sun-compass direction by means of a set of black screens. After rewarding the ants, the terrestrial cues were simultaneously displaced in such a way that the ants, when released, had to choose between the Sun-compass direction and the direction toward the black screens including an angle of 90°. They first followed the former direction but switched to the horizon landmarks with proceeding competition situations, as is true for the foraging runs. Even during the return runs no compromise directions were performed, furnishing further proof for our previous statement. While foraging, however, the ants learn the direct astromenotactic direction to a special point after reaching it in a roundabout way, but this does not hold for the return runs. When the horizon landmarks are removed, even after more than 20 competition experiments, the ants never follow the direct astromenotactic return course but choose the counter-direction of the immediately preceding foraging course. In contrast to the foraging situation, no integration and learning of astromenotactic angles seen at the return runs can be proved.

As the astromenotactic angle of the return run is determined by the counter direction of the foraging run, one may now ask whether a special constellation of horizon

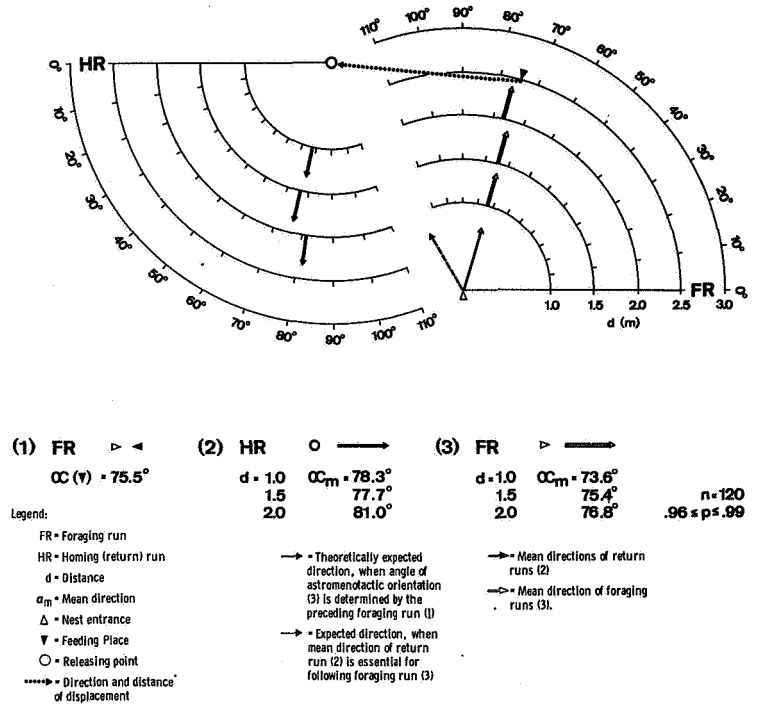

FIGURE 11. Competition between the astromenotactic angles of the preceding foraging run and the preceding homing run.

landmarks seen during the foraging run is also reversed for direction finding on the return run—more generally, whether terrestrial cues learned while foraging are also used during the return runs. Our experiments show that ants returning to the nest can only orient toward those horizon landmarks which they have seen during the preceding return runs, irrespective of whether or not these landmarks were presented during the foraging runs. From these and other experiments we may conclude that the direction of the return run is determined as the astromenotactic counter direction of the foraging run but not by the reversed constellation of horizon landmarks seen while foraging. The terrestrial cues used in the return situation must be separately learned during the preceding return runs. Similar results can be taken from experiments on maze learning in bees, wasps, and ants (*Apis mellifica, Vespa germanica,* ref. 36; *Formica schaufussi,* ref. 37). Other learning parameters (e.g., acquisition, retention, and reversal learning) cannot be discussed here in detail.[3]

What I wanted to show is that separate orientation mechanisms are responsible for the orientation of the desert ant (*Cataglyphis bicolor*) toward astromenotactic angles and horizon landmarks. If both sets of visual stimuli compete with each other, the ants switch over from one to the other orientation

[3] WEHNER, R.: Die Konkurrenz von Sonnenkompass- und Horizontmarken-Orientierung bei der Wüstenameise *Cataglyphis bicolor* (Hymenoptera, Formicidae). Zool. Anz. Suppl. (in press).

mechanism and do not perform a compromise direction. Depending on the physiological demands of the two mechanisms, the visual system may be topologically subdivided. Finally the storage of information presented by both sets of visual stimuli is restricted to special stages of the orientation runs.

DISCUSSION

QUESTION: What is the natural food of the ants and how do they forage?

WEHNER: In the regions where our experiments were performed (southern Tunesia), the natural food of *Cataglyphis bicolor* consists of desert beetles (e.g., *Tenebrionidae*) and other desert insects as well as amphipod crustaceans in areas near the coast. The ants reach their feeding places, which may be 100 to 200 m from the nest entrance, first in a straight course and then by searching around at random. The development of the well established learning capacities in these ants may have been supported by the necessity of foraging a freely moving prey, for a special feeding place can be kept constant only for a few foraging runs.

KLEERKOPER: Has the locomotor pattern of foraging ants been studied to any extent? Is there any indication that the moves are either random or programmed?

WEHNER: We have studied random movements by releasing ants from a point not known to them. They search at random in irregular, increasing circles. After searching around, they return to the point of original release. Therefore, no dislocation of the searching ant occurs in spite of the vast excursions performed by them.

WILLIAMS: What would happen if you deprive the ant of its Sun vision by a piece of cardboard?

WEHNER: The ant would orient quite exactly according to the pattern of polarized light in the sky. A comparable situation is established before sunrise and after sunset when the ants show a bimodal distribution of their orientation angles induced by the symmetrical pattern of polarized light at that time. This distribution suddenly switches over to an unimodal one when the Sun is visible above the horizon.

BULLOCK: What is the difference between ant and wasp behavior?

WEHNER: The solitary wasps (*Ammophila, Bembix, Philanthus*) studied by the Dutch school (ref. 38) react more precisely to natural landmarks as do *Cataglyphis bicolor* in the desert regions of southern Tunisia when confronted with artificial terrestrial cues. If *Cataglyphis bicolor* is displaced to a strange place, the ant will accurately run in the correct home direction and will search at random looking for the nest entrance after having performed a definite percentage of the real homeward course distance. Therefore, Sun-compass orientation mechanisms can be more precisely studied in these desert ants. Furthermore, that advantage is supported by the possibility of training the ants to special places and recording the orientation courses of the running ants (in contrast to the flying wasps). Additionally horizon landmarks can be presented in a definite way. Therefore, in *Cataglyphis* many orientation problems may be analyzed that are difficult to study with other insects such as wasps and bees.

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Visual Direction Finding by Fishes

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DIRECTION FINDING is a fundamental aspect of spatial orientation and navigation. Broadly it can relate to an animal's position in space, to its posture, and to the steering component controlling its locomotion. Sensory information about direction, which may be determined from a single external clue, is usually obtained by "distance receptors" as opposed to "contact receptors." Thus olfaction, hearing, vision, and mechanoreception mediated by gravity receptors are well known direction-finding modalities; electroreception and magnetoreception are less well known ones,[1] and in the latter case even problematical because no corresponding physiological receptor-transducer has yet been identified except in certain fishes.

The present review will consider only a limited aspect of direction-finding by restricting itself to underwater vision and to fishes. Furthermore, attention will be focused mainly on orientation in the absence of local landmarks and will also exclude general components like the dorsal light reflex.

Motivation for such a circumscribed approach is both practical and personal: practical in the sense of attaining a reasonable compromise between depth and scope, personal in terms of relating to our current research on polarized light perception in fishes (ref. 1) and the possibility that underwater polarization patterns in nature could provide an indirect Sun compass if the animals are able to use it (refs. 2 and 3).

Before dealing specifically with fish orientation, a brief review will be made of those characteristics of submarine optics that are particularly distinctive for seeing underwater. These mainly make visual direction-finding much more difficult than in air; hence, visual orientation is a challenge for aquatic animals. Nevertheless, the large, well developed eyes of most pelagic species in the photic zone attest to the adaptive importance of their vision.

UNDERWATER OPTICS

Except for bioluminescence, light in the sea (and other natural bodies of water) originates mainly from the Sun and to a much less extent from other celestial bodies as well as the sky. The air-water interface establishes two important features of underwater illumination. First, the difference in refractive index bends the rays of entering light and

[1] See Bullock, Lindauer, elsewhere in this volume.

causes total reflection in upward lines of sight beyond the critical angle. Thus the 180° horizon to horizon hemisphere of the sky is reduced to 97° (taking the water's refractive index to be 1.333) for an underwater eye; hence, all celestial clues to direction occur within this refraction cone, and the Sun rises and sets at apparent zenith distances of 48.5° instead of 90° as in air. Furthermore, as dictated by Snell's law, the apparent zenith distance is a nonlinear function of its real zenith distance in the sky.

Second, the fact that natural water surfaces are rarely flat calm means that ripples and waves will further distort, often markedly, the image of the celestial hemisphere. Thus the refracted Sun's disc usually appears as a more or less extensive glitter pattern comparable to, but much brighter near the surface and not subtending so large an angle, as the reflected glitter pattern observed looking down at the Sun's reflection on the water surface in air (refs. 4 and 5).

Once in the aqueous medium itself, radiant energy is then subject to absorption and scattering much more intense than in a clear atmosphere. As a result incident light becomes rapidly attenuated and less directional as it penetrates the water. For instance in Jerlov's type I clear oceanic water like the Sargasso Sea, surface irradiance (at 465 nm) is reduced to 1 percent at just over 140 m depth; in clear coastal water (Jerlov type 1) this 100-fold reduction occurs just above 30 m (ref. 6).

For the clearest deep oceanic water reported (at depths of 300 to 800 m in certain areas of the Indian Ocean (ref. 7), the 1 percent depth would be 219 m at the most penetrating λ, 475 nm Crater Lake (Oregon) approaches ideal clarity, and extrapolating the shallow measurements actually made would have its 1 percent depth at 292 m for 420 to 425 nm its most penetrating λ (ref. 8). Actually Crater Lake's transmittance at 475 nm is not as great as the Indian Ocean water cited.

Visibility

As a result of both absorption and scattering, visibility underwater is sharply reduced from that of clear air where 14 000 m of troposphere attenuate the incident solar radiation only to about 60 percent (ref. 9). In contrast to atmospheric visual ranges of 300 to 400 k, submarine ranges for large high contrast objects against a water background rarely exceed 100 m in very transparent water, while 40 m is more usual for quite clear water and 5 to 6 m typical for moderately turbid coastal waters (refs. 10 to 12).

At high light intensities the maximum range (in meters) for the human visibility of a large dark object viewed horizontally under water is roughly given by $4/c$ (ref. 13) where c is the total attenuation coefficient per meter (varies from 0.0158 to 0.033 for extremely clear natural water). Since contrast between object and background is crucial for visibility, depth will in fact be another parameter underwater. As depth increases overall irradiance decreases rapidly as cited above and scotopic contrast threshold for man is only about 0.1 as good as photopic (ref. 14).

The limiting case for submarine visibility would come at the depth where the Sun's rays are no longer detectable by an eye looking upward. If the attenuation coefficient were constant throughout the water column the irradiance at 840 m depth would be only 10^{-12} that at the surface even in Jerlov type I oceanic water. Depending of course on the eye and the detailed visual conditions, this could well be a plausible absolute threshold since estimates for maximum depths for eyes to detect sunlight in the clearest waters range from about 800 to 1500 m (refs. 7, 15, and

16). The deepest human daylight sighting from an experimental submersible is 700 m in quite clear water in the Bahamas (ref. 12). Since the world ocean averages nearly 4000 m in depth, three quarters or more of this huge living space is devoid of sunlight.

Directionality of Light

Both theory and field observations indicate that some directionality of the Sun's penetrating rays is maintained all the way down to the extinction depth. However, scattering and absorption cause the radiance distribution to become less directional than near the surface where it can be represented by a quasi-ellipsoid with its major axis parallel to the initial direction of the refracted ray. In deeper water the ellipticity decreases until the distribution resembles a prolate spheroid (ref. 6).

Perceiving the direction of maximal brightness, of course, requires discrimination between the visible intensities in neighboring areas of the radiance distribution. Thus, as the ellipticity of the latter is reduced and approaches a spheroidal shape, the potential accuracy of direction finding by this means will be significantly reduced. Again the rapid reduction of intensity with depth will have a marked additional effect since in general brightness discrimination deteriorates as illumination decreases. For man the minimum discriminable $\Delta I/I$ at scotopic light intensities is more than 10 times that at moderate photopic levels.

Despite the absence of appropriate data on fish visual physiology and behavior, Harden Jones (ref. 17) has made some interesting relevant calculations. Correlating measurements of underwater radiance distribution (for a fresh water lake) and estimates of the accuracy of human spatial localization and brightness discrimination, he calculates the Sun's bearing discrimination (within $\pm$ 20°) would reach threshold at a depth of 54 m; whereas Sun's altitude discrimination (within $\pm$ 10°) would similarly reach threshold at about 59 m. If these figures are of the right order magnitude, direction finding from the radiance distribution can be useful at best only in a shallow superficial layer.

In addition the combined action of scattering and absorption causes the zenith angle of the major axis of the radiance distribution to decrease from the angle of refraction at the surface to 0° at the so-called asymptotic or equilibrium depth. At this level the transmitted light distribution becomes symmetrical around the vertical. This occurs at various depths depending on the water's absorptance and scatterance (in turn strongly dependent on λ), e.g., at 100 m for green light in the Baltic and at 400 m for blue light in the Sargasso Sea (ref. 6).

Obviously when the angle between the main axis of the radiance distribution and the vertical falls below the threshold for an animal's discrimination, no azimuth directional information can be obtained from this factor at the corresponding depth and below. Even above the asymptotic depth, radiance distributions symmetrical around the vertical occur with the Sun below the horizon at sunrise and sunset, with the zenith Sun at noon and with a heavily and uniformly overcast sky.

Spectral Distribution

Whereas thin layers of clear water have little apparent effect on the visible spectral energy distribution of sunlight, thick layers have marked selective absorption reducing its bandwidth. In pure water or very clear seawater, this finally results in a narrow monochromatic band with a peak at 475 nm. In coastal waters and various fresh waters, "yel-

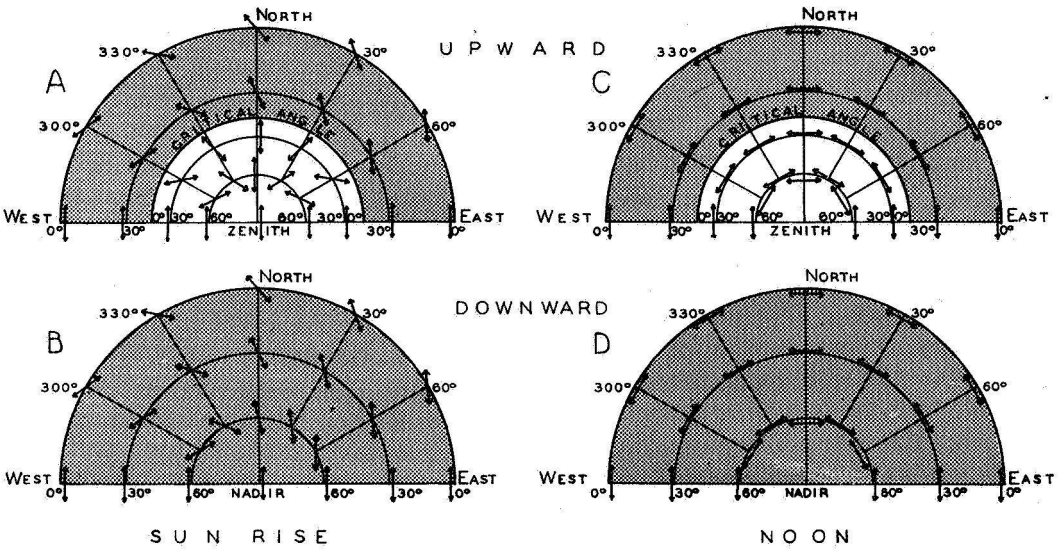

FIGURE 1. ***E*-vector patterns (double-headed arrows) in natural underwater illumination at sunrise (A, B) and noon (C, D). In upper hemisphere (A, C), sky polarization (as shown in the unstippled area) is visible in shallow water. Radial coordinate represents elevation (A, C) or depression (B, D) of the line of sight from horizontal; angular coordinate is the sight line's compass bearing. Within the critical angle (A, C), refracted apparent positions of the horizon as well as 30° and 60° elevation angles in the sky are shown (ref. 2).**

low substance" and other colored material in the water may alter the most penetrating λ to green, brown, or even yellow, orange, or red (refs. 6 and 18).

Clearly these wavelength characteristics of underwater light may affect contrast and have a powerful interaction with the λ_{max} of an eye's visual pigment. The wide range of λ_{max} shown by the visual pigments of various aquatic animals (refs. 14, 19, and 20) is no doubt a reflection of the adaptive importance of these light transmitting properties of the environment. Very marked effects on the maximum depth for seeing may be involved here (ref. 21).

Polarization

One interesting consequence of the scattering of light by water is the development of an underwater polarization pattern resulting from primary (Rayleigh) scattering of directional light (refs. 2, 22, and 23). Unlike the absorptance and the other results of scatterance, this optical feature of submarine illumination may increase the possibilities of direction finding by providing an index of the Sun's position down to depths of at least 200 m (ref. 24)—far beyond those where the Sun's disc is ordinarily visible as such and perhaps well in excess of those where the radiance distribution can be used to determine the Sun's bearing. (See Harden Jones' estimates cited above.)

In contrast to the situation in air where only the hemisphere including the blue sky is polarized by scattering of the Sun's rays, underwater light is polarized throughout the whole 360° solid angle, including near the surface the sky polarization visible above the

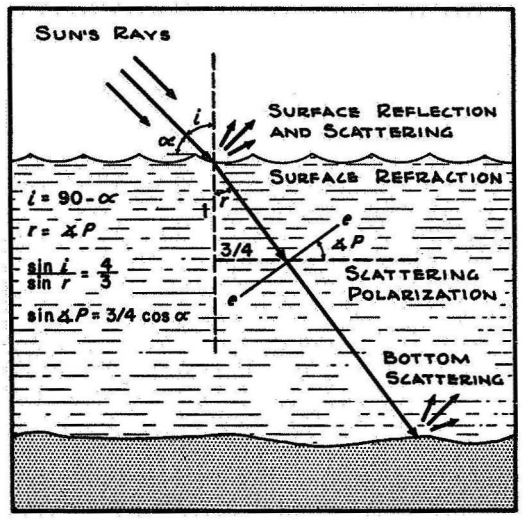

FIGURE 2. Origin of underwater polarization by primary scattering of directional light in the water. The overall *e*-vector pattern (fig. 1) arises from the interaction of this basic geometry with the Sun's altitude (fig. 4) and the relation of the lines of sight to the Sun's bearing (ref. 23).

critical angle (ref. 2) (fig. 1). The *e*-vector everywhere is normal to the Sun's rays in the medium (ref. 23) (fig. 2), and the degree of polarization ($p = I_{max} - I_{min}/I_{max} + I_{min}$) is maximal perpendicular to the Sun's direction (fig. 3). In this direction the tilt of the *e*-vector from horizontal is a simple function of the Sun's elevation angle (fig. 4).

As depth increases the changes in the radiance distribution toward the equilibrium depth condition can be directly observed by measuring the *e*-vector tilt in horizontal lines of sight perpendicular to the Sun's bearing (ref. 24). Theoretically at the asymptotic depth and below, the plane of polarization would be horizontal and 20 to 30 percent polarized in horizontal lines of sight while the vertical radiance from the surface would be unpolarized (refs. 25 and 26). However, polarization measurements to support this directly have yet to be made in deep water. The effect of depth on the degree of polarization has been measured only down to 115 m (ref. 27) (fig. 5) and as mentioned above, the *e*-vector orientation to a maxium of 200 m (ref. 24).

The degree of scattering polarization in pure water has a theoretical maximum of somewhat greater than 80 percent (ref. 6). *In situ* determinations of p due to scattering of the natural light have shown maxima near 60 percent for clear seawater west of Corsica and near Bermuda (refs. 27 and 28). Generally the values of p obtained with artificial light sources *in situ* are significantly greater than this presumably due to the stricter directionality of the artificial light (ref. 29).

Since polarotactic orientation in *Daphnia* has been demonstrated in the laboratory consistently for partial polarization of 20 percent and sometimes at 10 percent (Waterman and Jander, unpublished, cited in ref. 30), the naturally occurring polarized light underwa-

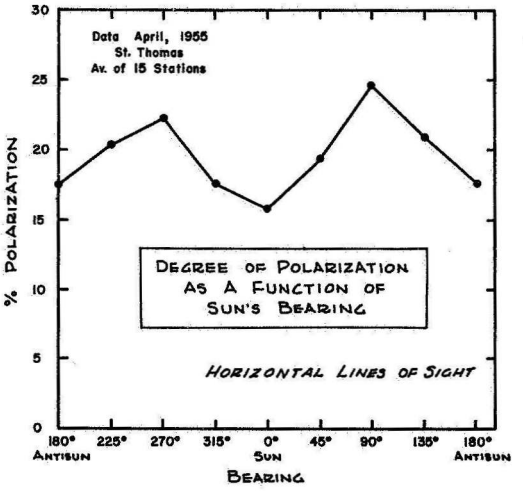

FIGURE 3. Dependence of the degree of underwater polarization (p) on the relation of the Sun's bearing to the line of sight. Obviously p is maximal normal to the Sun's direction. Lack of symmetry is due to the large variance in the field data plotted (ref. 23).

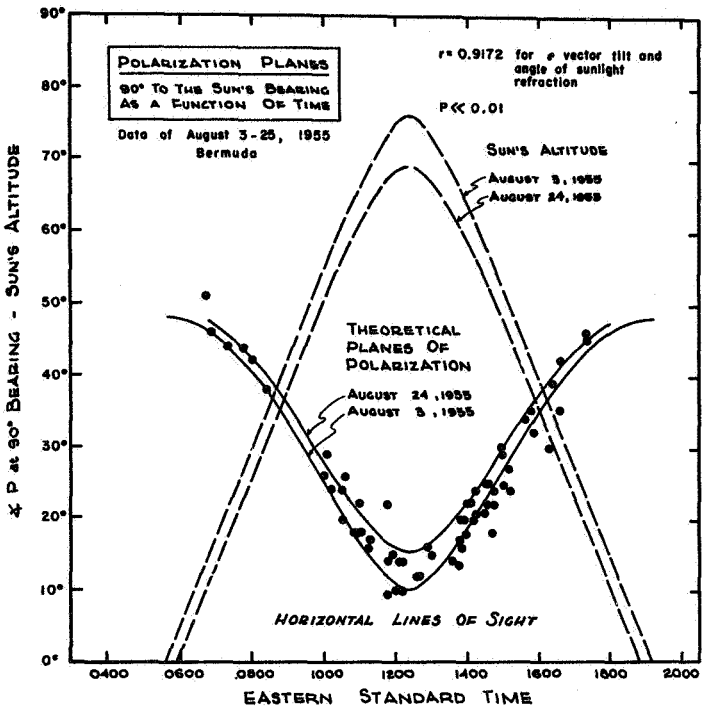

FIGURE 4. Effect of the Sun's altitude on the tilt of *e*-vector observed 90° to the Sun's bearing. Points represent the underwater measurements made at different times of day. Broken lines indicate the Sun's altitudes. Solid lines represent the corresponding angles *r* between the vertical and the refracted rays of the Sun predicted from figure 2; these are closely matched by the observed *e*-vector orientations (ref. 23).

ter has considerable biological interest as a possible Sun compass (ref. 3). Both the azimuth and altitude of the Sun could be determined rather easily from the *e*-vector tilt in horizontal lines of sight. The azimuth indication would be simple at all depths down to equilibrium, but altitude would of course show an interaction with depth as mentioned above.

Resumé

The net effect of these various features of underwater optics on visual direction finding may be briefly summarized as follows. Pilotage, i.e., steering by means of visible landmarks, is feasible only for littoral animals or benthic and parabenthic forms in the photic zone during the day. Since the water mass itself provides almost no aids to pilotage [but thermoclines and turbid strata are often visible (ref. 31)], other means of visual direction finding must be used throughout the great preponderance of the hydrosphere. As indicated above these will be either (1) celestial directional clues observed directly near the surface or observed indirectly through the radiance distribution down to levels no greater than the asymptotic depth or (2) alternatively the underwater polarization. The evidence for their use, as yet quite incomplete, is reviewed below.

CELESTIAL ORIENTATION

There are at least five different kinds of visual celestial cues which various animals can use for direction finding: the Sun (ref. 32), the Moon [2] (refs. 33 to 35), the stars (refs. 35 to 37), differential brightness of various parts of the sky (refs. 38 to 40) and the

polarization of the clear sky and natural waters (refs. 2 and 41). Because of lack of information on the likely significance of the other three clues for animals underwater only the first and last of the five are considered here.

The Sun Compass

Fishes, like many animals (refs. 17 and 42 to 46), are capable of finding a given azimuth by establishing and maintaining a fixed angular relation to the Sun's bearing. In so doing they are using the Sun's disc as a light compass as first proved in homing ants (ref. 32). At any given moment or for short intervals of time, this compass could function as a rather simple direction finder. The behavior involved would be like the transverse orientation of photomenotaxis (= light compass reaction) to an artificial light source (refs. 47 to 49).

However, over longer time intervals and for general use, a Sun compass must be much more sophisticated than a menotaxis because the movement of the Sun through the sky has to be taken into account. Also there is evidence that in some cases the Sun's altitude especially at local noon affects the direction finding (refs. 50 to 52). Therefore, knowledge of the Sun's path and a chronometer to measure its time course are required.

Time Compensation

In a variety of cases the Sun's course is compensated for not only during the day but at night when it cannot be observed, a capacity demonstrated when the animal is systematically orienting over 24 hr and allowing for the expected displacement of a stationary artificial Sun (refs. 50 and 53). For animals in the tropics where the Sun changes its direction of apparent movement with the season and for migratory forms which move from one hemisphere to the other the information required is particularly elaborate (for general discussion see ref. 54, ch. 8).

Time compensated orientation to the Sun was originally demonstrated for the honey bee and the starling by von Frisch (ref. 55) and Kramer (ref. 38), respectively. Similar solar direction finding was reported for the first time in fish (two species of centrarchids, *Lepomis gibbosus* and *L. machrochirus*) by Hasler, Horrall, Wisby and Braemer (ref. 56). Two types of training experiments in an experimental vessel exposed to the Sun and sky showed that these fish could use the solar disc to find a given geographical direction at different times of day.

Obviously the trained direction was a learned component of this behavior pattern, but was the Sun's path through the sky learned or genetically determined? Subse-

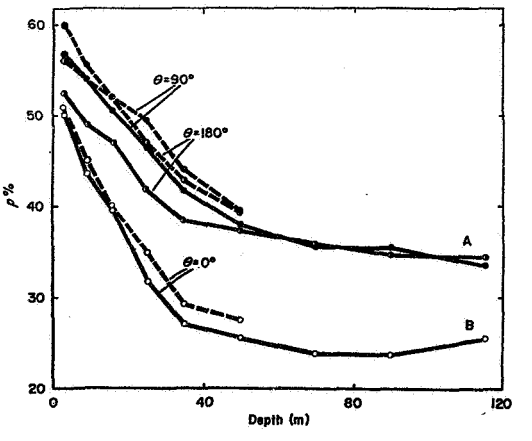

FIGURE 5. Effect of depth on degree of submarine polarization (p) in clear Sargasso Sea water near Bermuda (Secchi disc reading 50 m). Measurements were made in three lines of sight relative to the Sun's bearing (θ). Solid curves: measurements taken without filter; broken lines: with 500 nm narrow band filter (ref. 27).

[2] Compass orientation using the Moon has been recently reported for the mosquitofish *Gambusia* (Goodyear, 1971, in press).

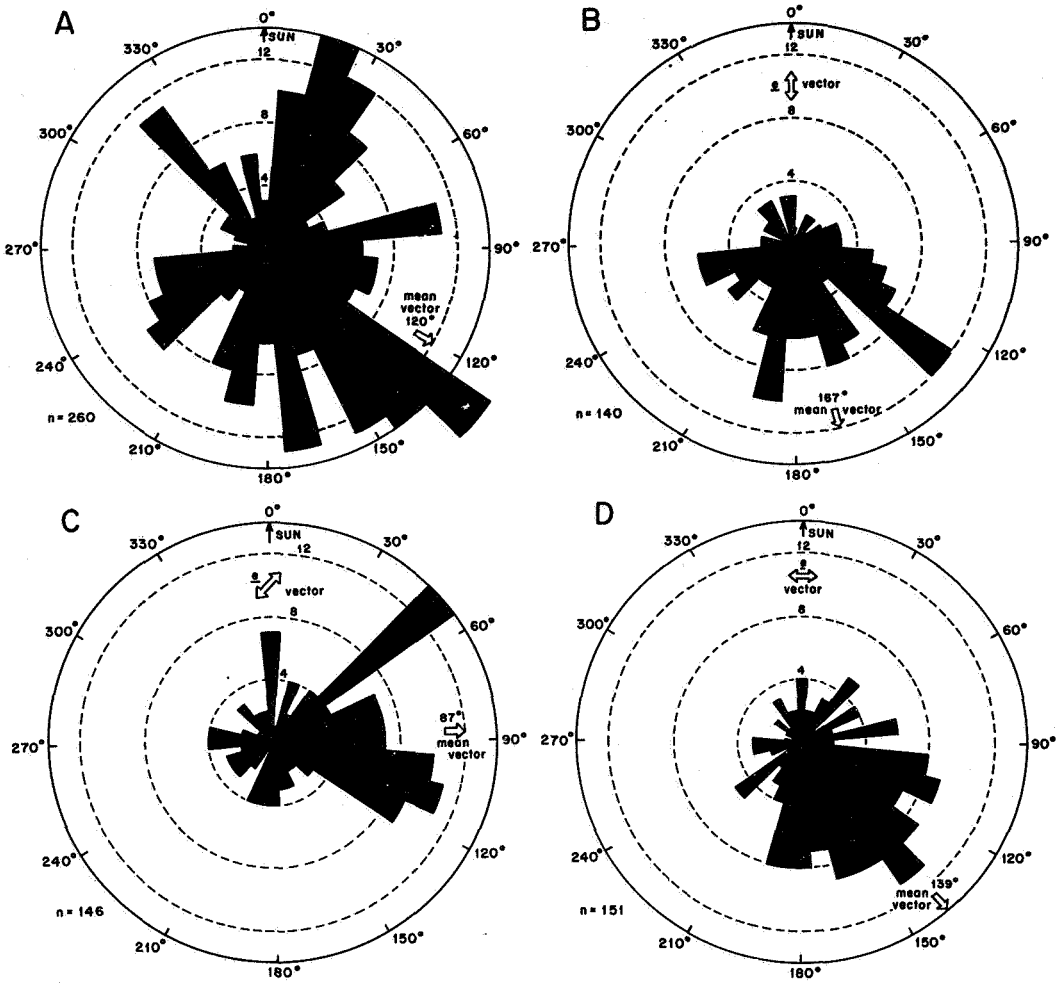

FIGURE 6. Directional orientation of the fish *Zenarchopterus* exposed to natural illumination underwater (A) and to this modified by an overhead polarizer with different *e*-vector orientations relative to the Sun's bearing at 0°. (*B*) *e*-vector 0 and 180°. (*C*) *e*-vector 45° and 235°. (*D*) *e*-vector 90° and 270°. Radial coordinate represents the number of observations grouped in 10° intervals. Mean vectors for the circular distributions are shown by single-headed broad arrows. The polarizer significantly modified these vectors in (B) and (C) compared to that with no polarizer added (A) (ref. 1).

quent work showed that fish raised without seeing the Sun were nevertheless able to compensate for its movement; therefore, the basic ability must be inherent. Furthermore, the compensation was appropriate to the season and latitude represented by artificial light-dark cycles under which the fish were kept (ref. 57).

Comparisons between the compensatory capacities of Northern temperate centrarchids and tropical cichlids demonstrated that the former always allowed for clockwise Sun

displacement which is all that is apparent in northern latitudes above the Tropic of Cancer. But the latter could compensate either clockwise or anticlockwise as would be required at different times of year within the tropics (ref. 52).

Occurrence in Fishes

Such direction-finding abilities have been demonstrated in fish orienting in experimental vessels or enclosures for *Lepomis* (3 spp.) (refs. 53 and 56), *Aequidens* (ref. 53), *Oncorhynchus* (refs. 53 and 58), *Cichlaurus, Uaru* (ref. 52), *Anableps* (ref. 59), *Anguilla* (ref. 60), *Gambusia* (ref. 61) and *Fundulus* (ref. 62).

Field experiments have also shown that displaced fish in lakes and marine reef areas can find the direction of their usual haunts by similar means (*Roccus*, refs. 56 and 63; *Scarus* (2 spp.), ref. 64; *Oncorhynchus*, ref. 65; *Salmo*, ref. 66). In some of these cases, complete sky overcast produced little deterioration in the orientation (*Anguilla* and *Salmo*), but in most instances orientation became random under this condition although the probability that there may have been other direction-finding modalities was usually not eliminated.

Thus there is no doubt that a wide range of fishes can use a Sun compass for direction finding. However, the field data, due to the difficulties of obtaining them are still rather thin, and the details of the relevant sensory and behavioral mechanisms remain largely to be discovered. For example, most of the experiments have been done in flat calm, very shallow experimental vessels where the shortcomings of submarine optics, discussed above, are minimal if not negligible. This has obviously been important in making it possible to prove the animals' basic capabilities but leaves open many real questions regarding their specific contributions to the overall functions of orientation and migration.

POLARIZED LIGHT COMPASS

If the preceding statement is true of the intensively studied Sun compass, how much more strongly does it apply to the possibilities of direction finding by underwater polarized light! Here even the basic capacity of fishes to perceive and respond to polarized light has been difficult to demonstrate. Indeed the failure to obtain strong behavioral or physiological responses has so far blocked progress towards understanding the sensory basis and biological significance of this visual capability. Nevertheless, we have recently begun field and laboratory experiments in this area which are making some headway.

Field work carried out in Palau in the Western Caroline Islands during the summer of 1969 showed that *Zenarchopterus* (a tropical West Pacific halfbeak) changed its orientation to Sun and sky when a Polaroid filter was oriented with the *e*-vector in directions different from the plane of polarization in the zenith sky (ref. 1). When the filter's *e*-vector was parallel to that of the zenith, i.e., perpendicular to the Sun's bearing, the spontaneous orientation behavior of the halfbeaks was not different from that without a polarizing filter (fig. 6).

Previous Evidence

Although we were somewhat surprised to find polarized light perception in a fish, there were several inchoate lines of earlier evidence which had suggested it. One of these stemmed from experiments done more than 10 years earlier on several fresh water and marine tropical fish. These were tested for azimuth preferences when exposed to a vertical beam of polarized light. For an animal

like *Daphnia* (refs. 67 to 69) or young cephalopods (ref. 70), which respond strongly to polarized light, the experimental procedure used produces marked peaks in the distribution of the animal's directions around a circle (fig. 7).

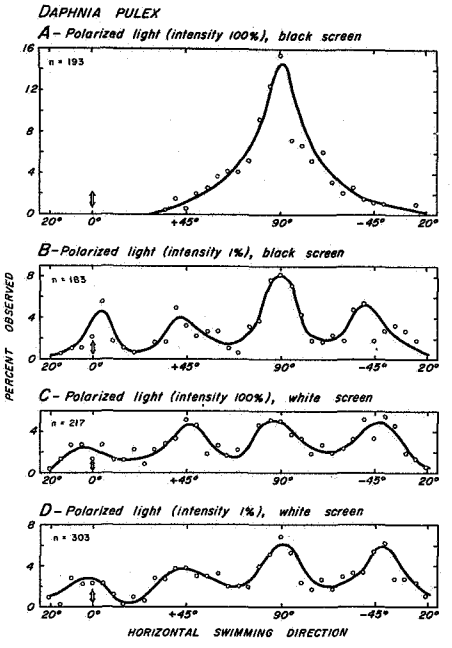

FIGURE 7. Polarotactic responses shown in the laboratory by *Daphnia* swimming in a vertical beam of polarized light. (A) Strong single-peaked orientation 90° to the *e*-vector observed with high light intensities and a black surround. Weaker responses with four peaks at 0°, 45°, 90°, 135° occur at reduced light intensities with the black surround (the light intensity effect) (B) or at both high and low light intensities with a white surround (the light contrast effect) (C, D). (Ref. 68).

In the fish tested, however, such marked orientation preferences to *e*-vector orientation were not found. Yet in some cases (e.g., the cichlid *Pterophyllum*), there was marginal evidence for a polarotactic response (ref. 71). But as rather extensive exploratory experiments failed to elicit stronger responses in this and other species, fishes were then abandoned by the author in favor of arthropods and cephalopods. Soon afterward the fact that some fish trained to use a Sun compass could continue to orient properly for some minutes after sunset was mentioned by Braemer in the discussion of his paper presented to the Deutsche Zoologische Gesellschaft (ref. 53). The fact that sky polarization arising from the primary scattering of the Sun's rays is at its maximum at such times was considered, but apparently no experiments to test its relevance were carried out.

Groot's Data

Somewhat later this same line of thought led to evidence in favor of a polarized light compass in the sockeye salmon (*Onchorhynchus nerka*). While studying the migration of smolts towards the outlet to the sea from Babine Lake and some other British Columbia lakes, Groot's interest was drawn to the fact that these fish were found to be migrating primarily during twilight when the zenith sky is strongly polarized (up to 90 percent) and the Sun's disc is not visible (ref. 58). In addition transposing the apparent position of patches of blue sky with a mirror appeared to have similar effects on salmon orientation to those found in *Apis* (ref. 72) for which the sky polarization pattern had definitely been proven to be important in direction finding.

Experiments on individual smolts exposed to the natural sky in 30 cm diameter by 30 cm tall cylinders of clear plastic were carried out by Groot at noon, afternoon, and twilight. No effects were noted except at twilight. Then rotating a polarizer placed over the vessel through 90° usually was followed by approximately the same angular direction change in the fish's headings. These headings,

however, were at various menotactic angles and not at 0°, 45°, 90°, 135° to the *e*-vector as in some arthropod and cephalopod basitactic responses to polarized light (refs. 70 and 68).

Also behavior with the polarizer present was different than with it absent. Thus with the *e*-vector perpendicular to the Sun's bearing the difference in behavior from the control (no polarizer) was greater than it was with the filter *e*-vector parallel to the Sun's bearing. This seems curious since in the zenith and, indeed, all along the great circle through the Sun and at sunset or sunrise the great circle perpendicular to that, the sky's *e*-vector is perpendicular to the Sun's bearing. Hence one might expect the least change from the no-filter condition with such an orientation of the imposed polarization. No explanation for this anomaly is available.

Dill's Experiments

Further support for a polarized light sensitivity in *Oncorhynchus* is provided by an unpublished master's thesis by Dill (ref. 73) who worked with Groot. Two kinds of laboratory experiments were done, again with smolts. One test was to see whether the fish's directional preferences were related to *e*-vector orientation when it was exposed to a vertical beam of polarized light. Comparison of the heading distributions shows that on the basis of a χ^2 test significant differences ($p < 0.01$) from random orientation occurred with a peak located at 22.5° relative to the *e*-vector when the polarizer was present but not when it was absent ($p > 0.05$). However, an explanation for this persistent menotactic orientation relative to the *e*-vector in a considerable number of fish tested at different times of day is not obvious.

On the other hand, although more individual fish showed a preferred direction of orientation with a polarizer present, this was not significantly different from the number of controls which had a preferred direction also. But the "concentration" of headings around the preferred direction was greater with the polarizer than without. Thus while the data are neither unequivocal nor completely explainable, the balance of evidence from this kind of experiment supports polarized light perception. However, the possibility was not checked that light intensity artifacts were involved (refs. 68 and 69).

In a second type of experiment, smolts were trained by Dill to distinguish vertical from horizontal *e*-vectors with food as a reward. After an initial training period, the cumulative rate of response to the reinforced *e*-vector (one target with vertical polarization) was clearly greater than that to the nonreinforced plane of polarization (three targets with horizontal polarization.) When the reinforcement was discontinued for the fourth target (now oriented like the others), the rates became the same showing that secondary clues of some sort were not producing the previous results.

While this series of experiments may indeed prove polarized light sensitivity in sockeyes, no control was established on possible reflection artifacts in the setup. This consisted of an octagonal clear plastic experimental vessel with four small square polarizers mounted vertically on alternate faces of the octagon and illuminated from behind. As the vessel was shallow and the polarizers near the bottom, a sharp difference in the bottom reflection would be expected with vertical (dark, due to minimal reflection) vs horizontal (bright, due to maximal reflection) *e*-vectors. However, no check on this artifact seems to have been made; hence the sceptic might well attribute the fish's learning to intensity differences rather than directly to *e*-vector perception.

CURRENT WORK ON HEMIRHAMPHIDS

Since our 1969 field experiments on *Zenarchopterus* (ref. 1), we have had during 1970 a second period of extensive field work as well as laboratory experiments on this genus in Palau. These data have been only partly analyzed and so cannot be reported here. However, we have meanwhile undertaken laboratory experiments at Yale on available related fishes. Again their analysis is not complete, and indeed the experiments themselves are not finished, but a preliminary report can be made on results already obtained with the fresh water halfbeak *Dermogenys* from South East Asia.

As mentioned above, finding an experimental procedure to evoke strong *e*-vector responses from fishes has so far proved rather difficult. However, a particular technique worked out by Richard B. Forward, Jr., in collaboration with the author, is proving reasonably productive. As employed with *Dermogenys* tests are being run as follows:

Mature *Dermogenys pusillus* Van Hasselt were obtained from commercial aquarists and kept on a 12 hr light-dark cycle with the light phase starting at 9 a.m. For the experiments individual fish are placed in a shallow cylindrical clear plastic vessel, screened laterally with a white surround and exposed to a downward vertical beam of light. This light beam has in its path a Polaroid filter (white light between 99 to 100 percent polarized) mounted together with two sheets of wax paper acting as a depolarizer (fully polarized white light scrambled to about 4 percent polarized). For testing the effect of *e*-vector, the depolarizer precedes the polarizer in the beam and randomly selected *e*-vector orientations were tested at 10° intervals over 180°. For control runs the polarizer precedes the depolarizer in the optic train, and the polarizer-depolarizer is again randomly oriented in 10° steps to eliminate possible artifacts relating to any unsuspected asymmetry it might have.

After a 5 min wait in the light for the fish to calm down, the light is turned off. Following 1 min in the dark, the vertical beam is turned on again and a sequence of 13 pictures taken at a rate of 1/sec by a camera viewing the experimental vessel from below. Polarized and depolarized tests are run alternately and eight sequences carried out on each individual fish. In the data here reported, 38 fish are included.

The directional behavior has been analyzed by measuring the direction of the fish's heading in each frame and correlating the number of "pauses" (counted as angular changes of 0° or 10° between successive frames) with the *e*-vector orientation in which they occurred.

While some of the runs look highly correlated with the polarization, others do not. Correspondingly the total data do not show significant preferential orientation. However, if the runs done in the morning are separated from afternoon runs, a significant difference does appear. Consequently, four categories need to be considered: AM polarized, AM depolarized, PM polarized and PM depolarized.

Only the first of these shows significant deviation from a random orientation (figs. 8 and 9). In the morning polarizer-present case peaks are present at 40° and 130° oblique to the *e*-vector. A χ^2 test shows that in this case the distribution is nonrandom ($p > 0.01$), but that the 40° individual peak does not differ significantly from the mean. However, since these data were obtained in the spring of 1970, 14 more *Dermogenys* have been run in the same way with similar results. Consequently the N's are now sufficiently large so that both the 40° and 130°

peaks can be shown to differ from the mean of all the angles tested at the $p > 0.005$ level.

Polarotaxis with 45° and 135° preferred directions has been observed previously in insects (refs. 73 and 74). Multiple peak basitaxes with preferred directions at 0°, 90° or 0°, 45°, 90°, 135° have been widely demonstrated in one water mite, a considerable range of crustaceans and insects as well as in cephalopods (ref. 75). Their occurrence implies interesting trigonometric processing of the visual information and the consequent motor output (ref. 76), but relatively little is known about this. One exception to such general ignorance is that the input for polarized light perception is known to be organized in two orthogonal channels in decapod crustaceans at least (refs. 77 to 83).

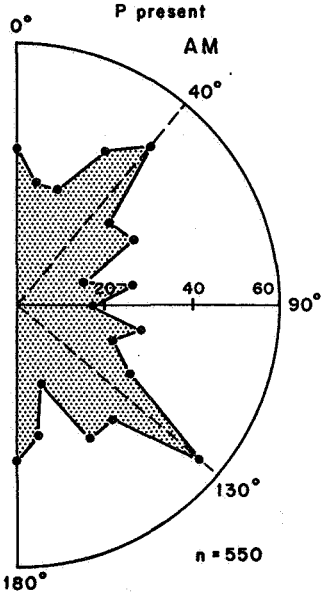

FIGURE 8. Polarotactic responses of the fish *Dermogenys* exposed in the laboratory to a vertical beam of polarized light. Clear maxima occurred at oblique angles to the *e*-vector (40°, 130°). This data was taken in morning experiments. Compare figure 9 (R. B. Forward, Jr., and the author, unpublished).

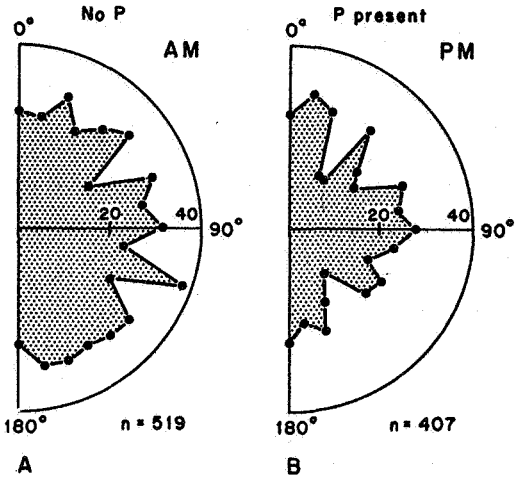

FIGURE 9. Absence of significant preferential orientation of the fish *Dermogenys* in control experiments in the laboratory using an unpolarized vertical light beam as well as in afternoon experiments with the beam polarized. (A) Not polarized, AM experiments. (B) Polarized, PM experiments. Compare figure 8 (R. B. Forward, Jr., and the author, unpublished).

PROBLEM OF MECHANISM

The similarity of the fish and insect oblique polarotactic pattern is an interesting parallelism particularly since the vertebrates in general lack the fine structural details that endow the rhabdom-bearing eyes of arthropods and cephalopods with their *e*-vector sensitivity. The critical matter here is the construction of the photoreceptor organelle (the rhabdom) out of a large number of regularly arranged microvilli that contain all or most of the visual pigment (refs. 82 and 84). For the single photoreceptor cell of which they are an elaboration of the cell membrane, all the microvilli are parallel to one another and perpendicular to the local optic axis of the

receptor. Direct microspectrophotometric measurement has shown in isolated crustacean rhabdoms that dichroism of the visual pigment, presumably effective because of the regularity of its molecular arrangement in the receptor membranes, allows individual cells to be differentially sensitive to *e*-vector orientation (refs. 82, 83, and 85) (fig. 10).

In contrast fish eyes, like those of other vertebrates, lack rhabdoms entirely and have their photoreceptor membranes organized in stacks of plates that are isotropic to polarized light traversing the outer segment axially as in normal vision. Consequently a retinal mechanism for *e*-vector sensitivity would appear to be lacking although the widespread occurrence of regularly arranged twin cones in teleost retinas (refs. 86 and 87) might somehow be involved.[3]

Retinal Mechanism

Fairly extensive measurements of receptor potentials, *s*-potentials, and ganglion cell spike frequencies in isolated fragments of goldfish retina have failed to disclose any significant polarized light discrimination.[4] The goldfish has not been proved behaviorally to respond to *e*-vector orientation, so perhaps our failure to record retinal responses to polarization is not surprising; yet if we accept the provisional evidence that cichlids, salmonids, and hemirhamphids can see polarized light, the capacity seems rather widespread in teleosts.

Indeed our negative results so far with the fish retina should not be considered definitive because repeated earnest attempts to record polarized light discriminating fibers in the optic nerve of decapod crustaceans did not produce convincing results on this point (refs. 88 and 89). Subsequently extensive data of various kinds were obtained for *e*-vector discrimination at the retinal level (in addition to the earlier behavioral evidence); and, recently in fact successful recordings from two categories of optic nerve fibers, maximally sensitive to orthogonal *e*-vectors, have been achieved in the crayfish.[5]

Extraretinal Mechanism

Of course, there is the possibility that polarized light responses in fish depend on some extraretinal mechanism. In man the perception of polarized light depends on the dichroism of the yellow macular pigment on the surface of the central retina, but this alternative is quite unlikely in teleosts since macular pigment is limited to primates (ref. 87). However, there is some evidence that the adipose eyelid present in many fishes is both birefringent and dichroic (ref. 90).

For example in the Pacific herring *Clupea pallasii* 40 percent less linearly polarized light is transmitted by the fresh adipose eyelid when the *e*-vector is vertical (i.e., parallel to the dorso-ventral axis) than when it is horizontal (ref. 90). Hence fish with such a structure over their cornea may be able to use it as an *e*-vector analyzer; but even if this were so, it does not solve the general problem. For one thing the *e*-vector discrimination found in *Oncorhynchus* was unaffected by adipose eyelid removal (ref. 73). However, only a small portion of the posterior adipose eyelid of salmonids (which is reduced compared to clupeids and some other teleosts) overlies the eye (ref. 90), so that Dill's experiment may not be a critical test of the general visual significance of this structure.

Furthermore the alternative that the *On-*

[3] G. D. Bernard, personal communication, 1969.

[4] H. Hashimoto, in collaboration with the author, unpublished, 1970.

[5] Yamaguchi, in press, 1971.

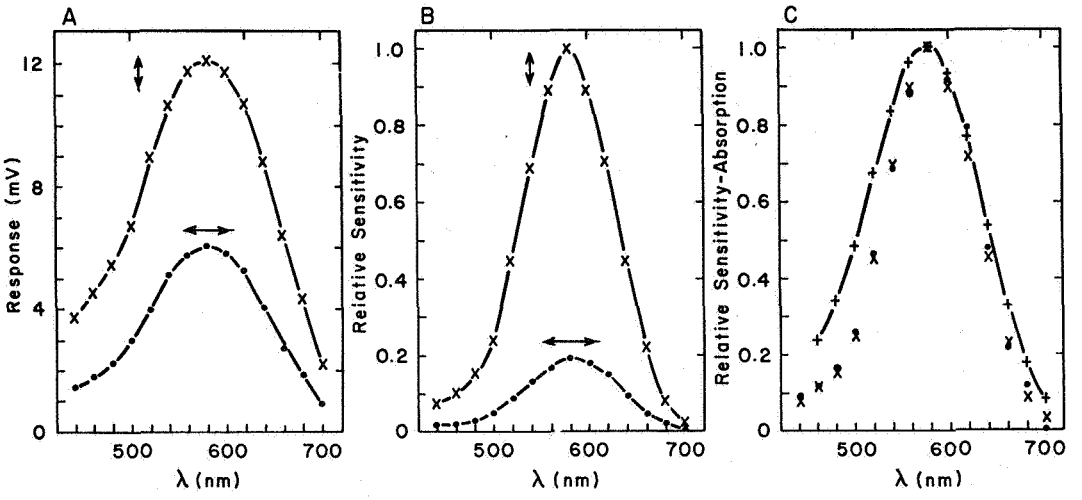

FIGURE 10. Differential sensitivity to polarized light in a single retinular cell of the compound eye of the crayfish *Procambarus*. This receptor cell had a λ_{max} at 580 nm and was 5.25× more sensitive to vertical (dorso-ventral) than horizontal *e*-vectors (shown by double-headed arrows). (A) Spectral response curves obtained from intracellular receptor potentials. (B) Relative spectral sensitivities calculated from A and the response energy curve. (C) Normalized relative spectral sensitivities for the two *e*-vector directions compared with the absorption spectrum calculated from the Dartnall nomogram for a vertebrate visual pigment with λ_{max} at 580 nm (ref. 83).

corhynchus adipose eyelid is too small to act in *e*-vector discrimination indicates that some other mechanism is responsible for the salmon's apparent perception of polarized light. This is certainly true of *Pterophyllum, Zenarchopterus,* and *Dermogenys* which lack adipose eyelids altogether. Nevertheless further study of possible polarized light responses in fish which do have well developed adipose eyelids seems highly desirable.

Another intriguing possibility is that some sort of extraocular sensory perception of light (EOP) might be involved in fish polarized light sensitivity. We know that in certain copepods their median naupliar eye can effectively analyze polarized light (refs. 91 and 92); but there, as in the arthropod lateral eye, regularly arranged microvilli are apparently involved in the mechanism (ref. 93). As possible analogs of the naupliar eye, the midbrain region, and its associated appendages, the parapineal (parietal) and pineal bodies may provide likely sites of EOP in fishes since all these are known to be light sensitive (ref. 94).

Yet no rhabdom-like membrane systems have been reported. Instead stacked lamellar elements resembling cone outer segments have been widely found, more specifically in the pineal (e.g., ref. 95). Although such structures in the retina are well known to be isotropic along their normal optic axis, rod outer segments are strongly dichroic for light transmitted perpendicularly to that axis (see discussion and references in ref. 82). However, no data on the occurrence and possible significance of these properties are available for fish pineal photoreceptor cells.

Alternatively the possibility that dichroism of the skin or skull over this region might

confer polarized light sensitivity on certain fishes has been considered.[6] But at least in *Zenarchopterus* no evidence for significant dichroism was found in the appropriate regions of freshly dissected specimens (ref. 1).

However, amphibians (*Acris* and *Ambystoma*) have recently been demonstrated to be capable of celestial orientation after their eyes have been removed but not when the midbrain region of the skull was covered by an opaque subdermal screen in blinded specimens (refs. 96 and 97). Also phototaxis and photokinesis in some fishes are affected by the pineal (e.g., refs. 94 and 98) but in other species are not (ref. 99). Thus there are several intriguing lines of research that need to be systematically followed up for their real relevance to the problems of visual direction finding by fishes.

SUMMARY

The particular conditions of underwater vision sharply restrict the scope of visual direction finding potentially available to fishes and other aquatic animals. These restrictions stem both from the rapid absorption of sunlight by the water which leaves 75 percent or more of the sea's volume without daylight and from the marked scattering of light even in the clearest of water which rapidly results in image deterioration.

One consequence of this scattering may, however, be of use in underwater direction finding, namely the Sun-dependent polarization patterns in the water. These can reach maxima of at least 60 percent polarization and have been proved photographically to provide clear evidence for the Sun's azimuth at depths down to 200 m which are considerably greater than estimates of maximum depths at which the Sun's disc or the submarine radiance distribution could be used for this purpose. The feasibility of such a time-compensated celestial compass has been repeatedly supported by the demonstration of a direct Sun compass in a wide variety of fishes (as well as other animals).

However, the relevance of the natural polarization pattern as a potential underwater Sun compass for fishes is problematic for several reasons. To begin with, demonstrating that fish can discriminate the plane of linearly polarized light has proved difficult because the behavior patterns used as evidence have been rather weak and the possibility of intensity artifacts has not yet been adequately controlled. Nevertheless there is an accumulating body of data supporting polarization perception in fish—more particularly our continuing field and laboratory experiments on tropical hemirhamphid teleosts. These should soon permit the testing of differential intensity effects and the demonstration of sensory mechanisms.

ACKNOWLEDGMENT

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DISCUSSION

GWINNER: Is it correct that the altitude of the Sun could enter into the orientation pattern through polarized light?

WATERMAN: Yes. Braemer and Schwassmann showed that cichlids would change their behaviorally conditioned direction if the apparent altitude of the Sun was modified without altering its bearing. They used a mirror to reverse the Sun's apparent direction by 180° and then changed its apparent altitude by tilting the mirror. They did get a significant shift in the fishes' directional behavior. Since the Sun's altitude, as well as its bearing, affects the underwater polarization pattern, it could also influence orientation there.

[6] T. Kuroki, personal communication, 1968.

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SESSION V

Sensory Mechanisms—Chemical Senses

Chairman, HOWARD E. WINN

Orientation Through Chemo-Reception in Fishes

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INCREASING NUMBERS of research reports continue to stress and document the role of the chemical senses in fish behavior. The behavioral patterns in which chemical stimulation has been shown to be important or even indispensable already cover virtually all phases of the life history of these animals. The capability to chemically discriminate, frequently at inconceivably low thresholds, prey, predator, food, nest, young, individuals of the same or other species, sex, water quality, and other conditions has been well-documented for a large number of species. Although olfaction is by far the more sensitive of the chemical senses and is required for the perception of the stimuli involved in most of the behavioral patterns mentioned, it has been demonstrated recently that, in some instances, the sense of taste can be the sole sensory modality necessary (ref. 1). There is ample evidence that olfaction is indispensable for the successful homing of anadromous fish, at least during their upstream migration (refs. 2 and 3).

It will not be necessary here to rehearse the dramatic and well-known spawning migrations of the Pacific and Atlantic salmons and their land-locked cousins. The ability of the individual fish of these species to return for spawning, after prolonged absence in the ocean or a lake, to the specific sites of their birth has been well-documented, and a number of experiments have demonstrated that anosmic animals are unable to perform this feat. Particularly, compared to controls, they are unable to make the correct choice of direction as they reach a fork of the river in the course of their upstream migration.

Under experimental conditions, chemical stimulation frequently affects the locomotor behavior of the animal and may result in so-called random movements often referred to as alarm or appetitive responses. The term "so-called" is used intentionally in that the designation "random" has been based on the gross appearance of these movements when visually inspected. However, more precise analyses of the parameters of many such locomotor patterns in some sharks and teleosts have demonstrated that, at least in the species studied, the movements are not random but have rather rigidly organized characteristics (ref. 4). On the other hand, many of the behavioral patterns elicited by olfactory stimulation comprise directed movements which are oriented either in relation to the source of the odor or to other environmental cues.

The descriptive but extensive documenta-

tion of the widespread significance of the chemical senses, particularly of olfaction, stands in great contrast to our ignorance about almost all the underlying physiological mechanisms. As to the peripheral transduction of the olfactory cell membrane, theories abound, and although promising progress is being made, there is no acceptable explanation for the phenomenon of odor perception. The central and possibly peripheral decoding systems which, in many species, allow for the discrimination of thousands of odorous substances, isolatedly and in mixtures, is as yet not understood. As to the mechanisms of orientation through olfaction in fishes, the topic of this paper, we are not much better informed.

In most behavioral responses to olfactory stimulation, cited earlier, directed movements occur, such as the approach by the predator to the odor source of prey and the upstream spawning migration of the salmon. There are many other similar responses, all of which are abolished or greatly modified in anosmic animals. The main problem these directed movements pose—a problem not limited to fishes—is the difficulty to define the orientation mechanisms involved since the molecular concentration gradient of an odor source does not contain vectors that can be used as directional cues by an animal surrounded by the field. Thus we must look for other means of orientation in these instances.

In the course of an earlier study on orientation behavior in some species of shark and a teleost, it was established that in multiple-choice situations none of the animals tested was able to locate the source of odor of a preferred prey when this was released from one of 16 compartments placed radially along the periphery of a cylindrical tank. From each compartment water flowed through an open gate toward an overflow located in the central open area of the tank. However, when the rate of flow of water from the compartment releasing the odor was increased slightly, the animals located the source of the odor quickly and without error although increase of flow without odor stimulation did not affect the animals' locomotor patterns. It may be concluded, therefore, that the role of odor perception in a concentration gradient is limited to that of a sign stimulus which, in the experiments in question, releases positive rheotaxis (ref. 4). It is likely that in different circumstances the same sign stimulus may release response to other directional cues. This mechanism would seem particularly appropriate to explain the role of olfaction in the orientation of salmon and other species in the course of their upstream spawning migration. The fish within the odor gradient released by the home ground would remain positively rheotactic as long as the specific odor substances were present. When presented with the crucially important choice of direction at a fork of the river, only the "correct" branch of the fork would contain the olfactory sign stimulus to maintain the rheotactic response. Entry into the "wrong" branch would eliminate the stimulus, abolish rheotaxis, and cause the animal to be brought back to the fork. The problem of orientation in a gradient does not arise. Behavior at river forks of migrating, normal, and anosmic salmon seems to be consistent with the proposed mechanism.

In nature, odor substances are not likely ever to be distributed in a smooth concentration gradient. Flow characteristics, differences of temperature, turbidity, density, viscosity, radiation, the positions of affluents, bottom contours, to mention just a few, produce discontinuities in many or all of the physical and chemical characteristics of a body of water. Therefore, a uniform spatial distribution of substances, including odorous substances, is unlikely. Even for rivers, the

existence of discontinuities in the characteristics of the water mass is well-known. In lakes this condition is, of course, still more pronounced. If it is considered, furthermore, that many biologically significant odors are released by spatially and temporally discrete sources, it becomes clear that a swimming fish will intermittently, probably very frequently, encounter and pass through odor concentration gradients whose boundaries are determined by the animal's thresholds for the substances involved and by the physical and chemical factors that affect the spatial distribution of the odorous substances. At many of these encounters, the animal will have to respond promptly and adaptively with directed locomotor responses. Once more, the problem as to the nature of the mechanism of orientation is before us. Various kineses and taxes, classified and discussed by Kühn (ref. 5), Fraenkel and Gunn (ref. 6), Kennedy (ref. 7), and others, particularly in respect to invertebrates, have been considered as possible mechanisms by investigators of this problem. However, the theoretical and experimental results are inconclusive and little agreement has been reached so far.

In the light of recent studies in our laboratory on the locomotor behavior of fishes, it seems probable that the difficulties arise from the limitations of conventional methods of observation and analysis which have been applied to the problem in the past. It seems obvious that an understanding of the mechanisms underlying oriented responses to environmental stimuli must be dependent above all on our ability to record these responses adequately. However, none of the methods used in the past seemed adequate to monitor locomotor behavior of fish during extended periods and with the accuracy and detail required for an analysis in depth of the locomotor patterns and their parameters. This rationale was the incentive for the design and

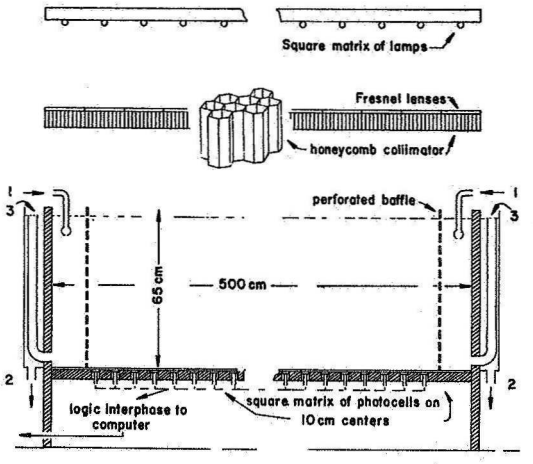

FIGURE 1. Schematic cross section of the monitor tank.

development in our laboratory of a system for the acquisition and processing of accurate data describing the locomotor behavior of fish in a spacious experimental environment appropriately controlled. The system was described in some detail earlier (refs. 8 to 10). Recently the technique allowed us[1] to obtain information that may contribute to the solution of the problem of orientation to chemical cues in fishes. It seems useful, therefore, to quickly outline the basic approach developed in the technique in question.

The movements of a single fish are monitored by means of a square matrix of 1936 photoconductive cells, on 10-cm centers, embedded in the floor of a tank measuring 5.0 × 5.0 × 0.5 m (fig. 1). A collimated light field illuminates the cells uniformly from a suspended ceiling above the tank at a color temperature of 2300 to 2400° K. Interception of the light by the fish sharply increases the electrical resistance of the photo-

[1] TIMMS, A. M.; AND KLEEREKOPER, H.: The Locomotor Response of Male *Ictalurus punctatus*, the Channel Catfish, to a Pheromone Released by the Ripe Female of the Species. Unpublished, 1970.

cell affected, an event which forms the input for an electronic logic interface with an on-line computer (fig. 2). The latter is programmed to establish the address of the photocell in the *x,y* matrix and the time of the event. These raw data are recorded on magnetic tape for subsequent analysis by the same or a larger computer but can also be processed in the course of the experiment by the computer on line which puts out on a teletypewriter, event by event, information on the velocity, absolute orientation in the tank, change of direction in radians, distance covered, and left- or right "handedness." The locomotor patterns can be plotted and are continuously displayed on a cathode ray tube. The linear resolution for the smallest target (3 mm) which can affect the resistance of a photocell in the conditions described is 10 cm. For a fish 30 cm long, the approximate minimum size generally used in our work, the angular resolution is not less than 4°. The effects of consecutive targets on a same photocell are discarded by the computer programs so that minor, repetitive movements of parts of the body, which do not produce locomotion, do not enter into the computations. By appropriate programming the information can be fragmented temporally and spatially so that behavior in a specific area of the tank (for example, that affected by a source of chemical stimulation) may be compared with that in other areas.

The manner in which water is supplied and odors or other chemical stimulants are introduced is important. Perforated panels, placed vertically along the four walls of the tank, form 20-cm-wide, peripheral channels. Water enters any one of these through a large number of small holes in a horizontal supply pipe and is admitted to the main body of the tank through the perforations of the panel; it then traverses the tank, commonly at a velocity of 1.6 cm/min, and leaves

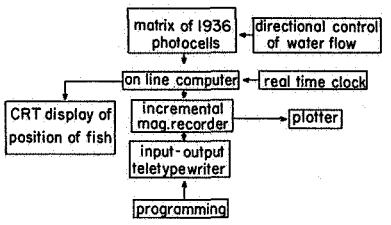

FIGURE 2. Flow sheet of data-acquisition and processing.

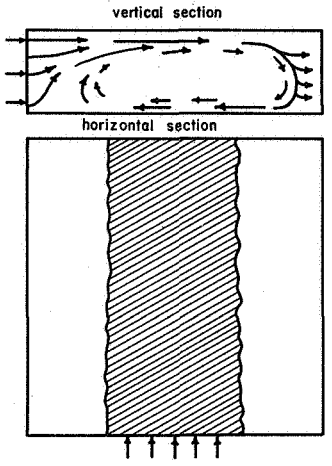

FIGURE 3. Sketch of flow pattern in the monitor tank.

through the perforations of the panel of the opposite channel where it discharges through an overflow pipe. By dividing the supply channel into three noncommunicating compartments of equal size and admixing a source of chemical stimulation in the central compartment, a "curtain" of the chemical stimulus is formed which, according to three-dimensional conductivity, temperature profile, and dye flow measurements, maintains its lateral boundaries with a high degree of stability and little diffusion until it reaches the vicinity of the discharge panel where it spreads out laterally. Vertically the flow pattern is more complex; its hydrodynamical and diffusion profiles are being studied in

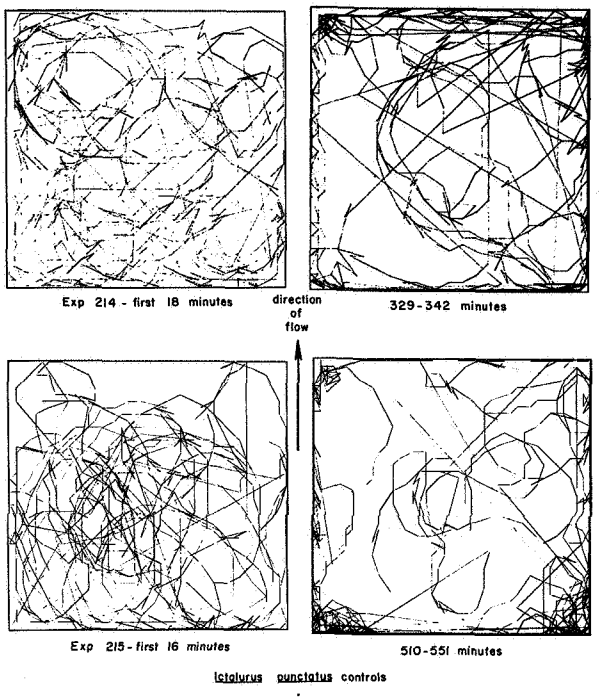

FIGURE 4. Locomotor patterns of *Ictalurus punctatus* prior to release of the female's pheromone.

detail in collaboration with fluid mechanics specialists. However, for the purposes of this paper, it may suffice to outline the flow pattern at the hand of figure 3 which is based on calculations by D. J. Norton, Department of Aerospace Engineering, Texas A&M University.

With this equipment we made some observations, referred to earlier, on the following phenomenon. In the breeding season, ripe males of the species *Ictalurus punctatus,* the channel or spotted catfish, are strongly attracted by the odor of mature females around which they quickly aggregate. This behavior is well-known to fishermen of the Mississippi who easily catch large numbers of the fish by placing mature females in a cage in the river. Recently we monitored this rather spectacular locomotor response by means of the technique just described.[2] Following a 12-hr monitoring period of a ripe male in the experimental tank, water from a container holding a ripe female was admixed with the supply in the middle compartment of one of the channels. Figure 4 represents plots of the locomotor patterns of two males prior to the release of the female pheromone. The left-hand plots correspond to the initial periods of the experiments; those to the right were made 311 and 494 min later, respectively.

Figure 5 illustrates the response of the male to the female odor; the left-hand plots cover periods of, respectively, 18 and 30 min immediately following the admission of the odor into the central compartment of the supply channel. The response is illustrated in greater temporal detail in figure 6. As soon as the fish entered the odor field (which in ex-

[2] TIMMS, A. M.; AND KLEEREKOPER, H.: The Locomotor Response of Male *Ictalurus punctatus,* the Channel Catfish, to a Pheromone Released by the Ripe Female of the Species. Unpublished, 1970.

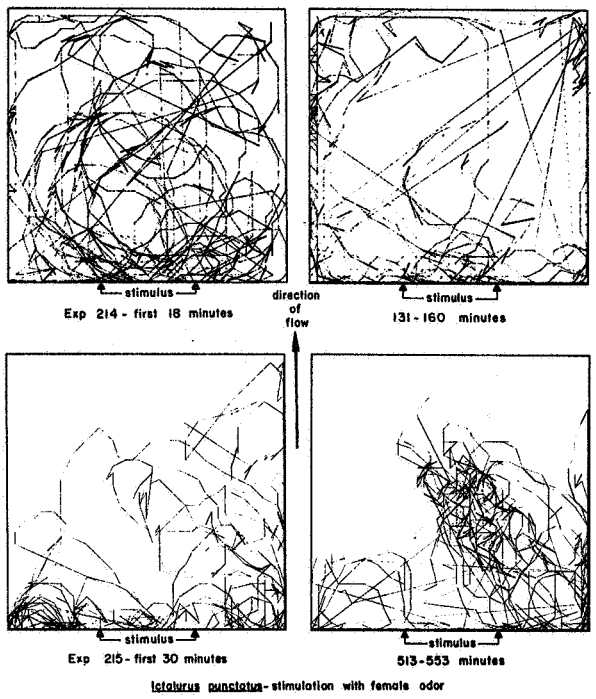

FIGURE 5. Response of a male *Ictalurus* to the female's pheromone.

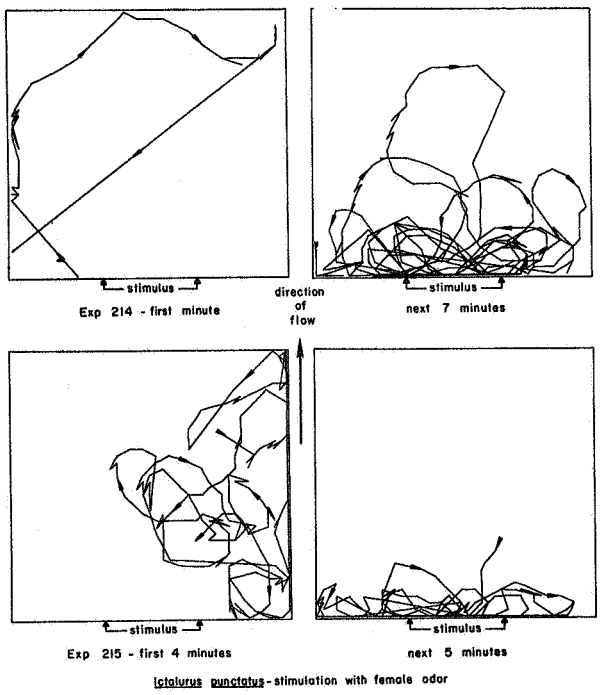

FIGURE 6. Part of same response as in figure 5 but resolved into shorter periods.

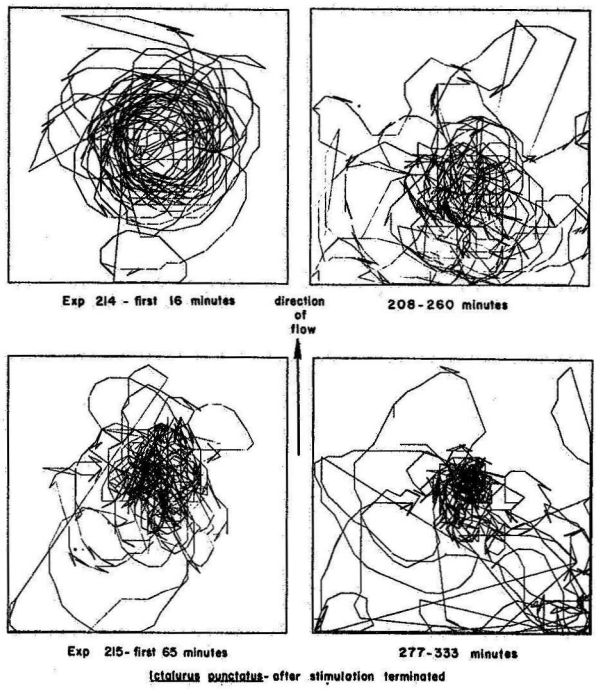

FIGURE 7. After interruption of the odor supply, the male follows the remaining odor patch in the tank.

periments 214 and 215 required 1 and 4 min, respectively), they restricted their movements mostly to the immediate vicinity of that section of the wall through which the stimulus entered the tank, rather than extending their locomotion to the much larger area of the tank affected by the female's odor. The resulting locomotor patterns are those of the right-hand plots of figure 5, which correspond to periods of from 2 to 7, and 5 to 9 min after the start of the chemical stimulation. These patterns consist mostly of forth and back movements parallel to and along the whole length of the section releasing the odor; on the plots this pattern is represented by a single, heavy line drawn by the pen of the plotter as it retraces repeatedly the same trajection.

The orientation mechanism that most readily accounts for the behavior described is that of tropotaxis by which the animal simultaneously compares the intensity of the odor in the two olfactory sacs and turns toward the side of the strongest stimulus. Since the perforated wall does not allow the fish to turn, locomotion remains closely parallel to the wall until the stimulus is lost, that is, at either extremity of the odor-releasing section of the channel. The animal then moves away from the wall, subsequently becomes "trapped" again in the odor field, and the process is repeated.

Strong support for this interpretation is provided by the behavior of the fish following the interruption of the female odor supply (fig. 7). The male immediately leaves the area along the wall and proceeds in continuous, almost perfect circles at some distance away from the wall but within the pathway of odorous water that moves from the central compartment of the supply channel, across the tank, toward the opposite wall of the

tank. As soon as the odor supply is cut off, "normal" instead of odorous water leaves this compartment pushing the mass of odorous water, released previously, ahead of it. As long as the stimulus strength is above threshold for this behavior, the fish remains entrapped in this odor "blot" as it moves across the tank. The perfect circus movement now displayed by the fish is entirely based on chemical cues and is difficult to explain by any mechanism but tropotaxis.

It has been stated repeatedly, but without experimental support, that tropotaxis, particularly chemotropotaxis, could only operate if the paired sensory organs were widely separated. "How widely" is the question that must be answered. In general, the capabilities of sensory organs and their central correlates have been consistently underestimated and the disbelief in a sensitivity that would enable closely placed, olfactory sacs to discriminate odor quality and quantity bilaterally seems to have precluded serious inquiry into tropotaxis as an orientation mechanism. In this connection it is particularly interesting that several authors (refs. 11 to 13) have reported the presence of free nerve endings of the trigeminal system in the olfactory epithelium of fishes. In some other vertebrates these trigeminal fibers have been shown to be odor-sensitive (ref. 14), and it is suspected that, in varying degrees, all odorous substances stimulate the trigeminal as well. Recently Schneider and Schmidt (ref. 15) found that, in man, the source of those odors for which the trigeminus endings are particularly sensitive can be located more accurately than that of odors which do not stimulate the trigeminus or do so to a lesser degree. They attribute the capability of source localization to the trigeminal neural pathway which, in contrast to the olfactory system, has a unilateral central connection so that inputs from left and right nostrils are processed independently in the central nervous system. Thus differences in time and/or concentration of stimulation between the lateral sense organs may be used for the localization of the source of an odor in a manner analagous to the mechanism of sound localization. A finding of particular interest is the long-lasting response of the animals to the pheromone odor. This is in direct contradiction to the often-stated "fast" adaptation of olfactory systems generally. Adaptation is either non-existent in *Ictalurus punctatus* or is prevented by intermittent exposure of the sensory epithelium to the odor. We do not know this yet, but the prolonged behavioral response exhibited by these fish should caution us against dismissing olfaction as a possible long-range orientation mechanism.

A tropotactic orientation system does not necessarily have to result in circular movements as displayed by *Ictalurus punctatus*. A few years ago, we observed that in *Ginglymostoma cirratum*, the nurse shark, the pathways leading to an odor source very frequently were part of a logarithmic spiral. Similar observations were made and tested mathematically in other species[3] (fig. 8). In such animals the two lateral olfactory organs may be part of a target-seeking mechanism similar to that of the theoretical model developed by F. Brouwer[4] in which the vehicle describes a logarithmic spiral pathway in approach to the target.

It may be mentioned, incidentally, that the circular movement described by *Ictalurus punctatus* is consistently dextrous. Whether or not this is related to the observed prevalence of right-handedness (predominance of right-hand turns) in the normal locomotion of these animals remains to be ascertained.

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[3] KLEEREKOPER, H.; ANDERSON, V. M.; AND TIMMS, A. M.: Logarithmic Spiral Components in Locomotor Patterns of Fish. Unpublished, 1970.

[4] BROUWER, F.: Stewart-Darmer Corp., Unpublished.

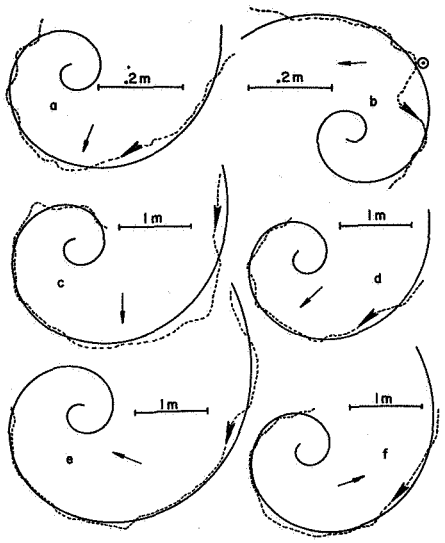

FIGURE 8. Pathways of *Ginglymostoma cirratum* describing logarithmic spirals.

It has been pointed out (ref. 16) that discontinuities in the water mass of a river system would make it difficult, if not impossible, for a fish in upstream spawning migration to be guided by the olfactory perception of spawning ground odors that may locally disappear at such discontinuities. If, however, chemotropotaxis becomes operative on these occasions, this difficulty should disappear since the fish would be able to orient so as to remain within the odor field which, in turn, would sustain positive rheotaxis. It would seem that these two orientation mechanisms should be entirely sufficient to maintain the migrant on its upstream course.

However, not all observed oriented movements can be explained by the two mechanisms discussed so far. For some time now we have been engaged in an analysis of locomotor responses by 30-cm-long goldfish to nonbiological chemical agents such as ions of heavy metals and sodium chloride at very low, sublethal concentrations (maximally 25 μg/1 metal ion), using the methods already mentioned with minor modifications. Again all the locomotor parameters within and outside the chemically affected areas of the monitor tank were measured, compared, and the differences tested for statistical significance. A report on this work is forthcoming.[5] Suffice it to state here that the fish, on entering the water mass containing $CuCl_2$ (with NaCl of the same molar concentration as the control), modifies only one of the many locomotor characteristics analyzed. There is a significant positive deviation in the headings of the movements in response to the copper ions against the direction of the flow of the water.

DISCUSSION

QUESTION: How do these results compare with those reported in your paper in *Nature*?

KLEEREKOPER: We have made additional observations under different conditions, and the results presented in *Nature* still stand. We have further evidence that in spite of an apparently irregular locomotor pattern, approximate equality in cumulated left- and right-hand turns is maintained. In other words, the animal moves about but seems to be able to keep track of its deviation from the straight line of progression and to compensate for these by turns in the opposite direction. This is neither a random phenomenon nor does it result from the presence of the walls. Angle compensation occurs also in stagnant water and is, therefore, not an effect of water current.

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The Case for Long-Range Chemoreceptive Piloting in *Chelonia*

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THE RECENT SUGGESTION that chemoreception may provide the latitudinal component of the open-sea guidance mechanism of the South Atlantic green turtle (ref. 1) has not been subjected to test. The straightforward way to test the assumption would be to monitor sensory responses of migrating turtles through electronically tracked and telemetered journeys to the island breeding ground (fig. 1). Efforts to do this have not yet been successful, and the case for piloting by chemical cues still rests on circumstantial evidence. This paper considers some aspects of that evidence and suggests ways in which the known ecology of the species bears upon the search for a theory of island-finding navigation by an aquatic, airbreathing animal.

OCEAN CURRENTS AND THE ECOLOGICAL GEOGRAPHY OF THE GREEN TURTLE

Three problems in the reproductive ecology of sea turtles, under scrutiny since the program of marine turtle research at the University of Florida began, are (1) to explain why certain small islands or restricted sections of mainland shore are chosen by *Chelonia* as nesting grounds, even when located a thousand miles or more from the year-around feeding ground of the population (figs. 1 and 2); (2) to identify guidance mechanisms used by the migrants in their periodic open-ocean travel to those places; and (3) to account for the so-called "lost-year"—the virtually complete disappearance of young sea turtles during their first several months of life. It seems increasingly clear that the three problems are closely related.

In the search for an answer to the site-choice question, beach topography, the physical character of the nesting medium (refs. 2 to 4), differential immunity to predation and to past human depredations, and even paleogeographic changes (ref. 5) have all been considered as possible factors, but many cases of breeding-site selection remain wholly anomalous. It now seems possible that these will be explained only if answers to the second and third questions listed above can be found.

As information from tagging and field surveys accumulates, it appears increasingly likely that ocean currents are fundamentally

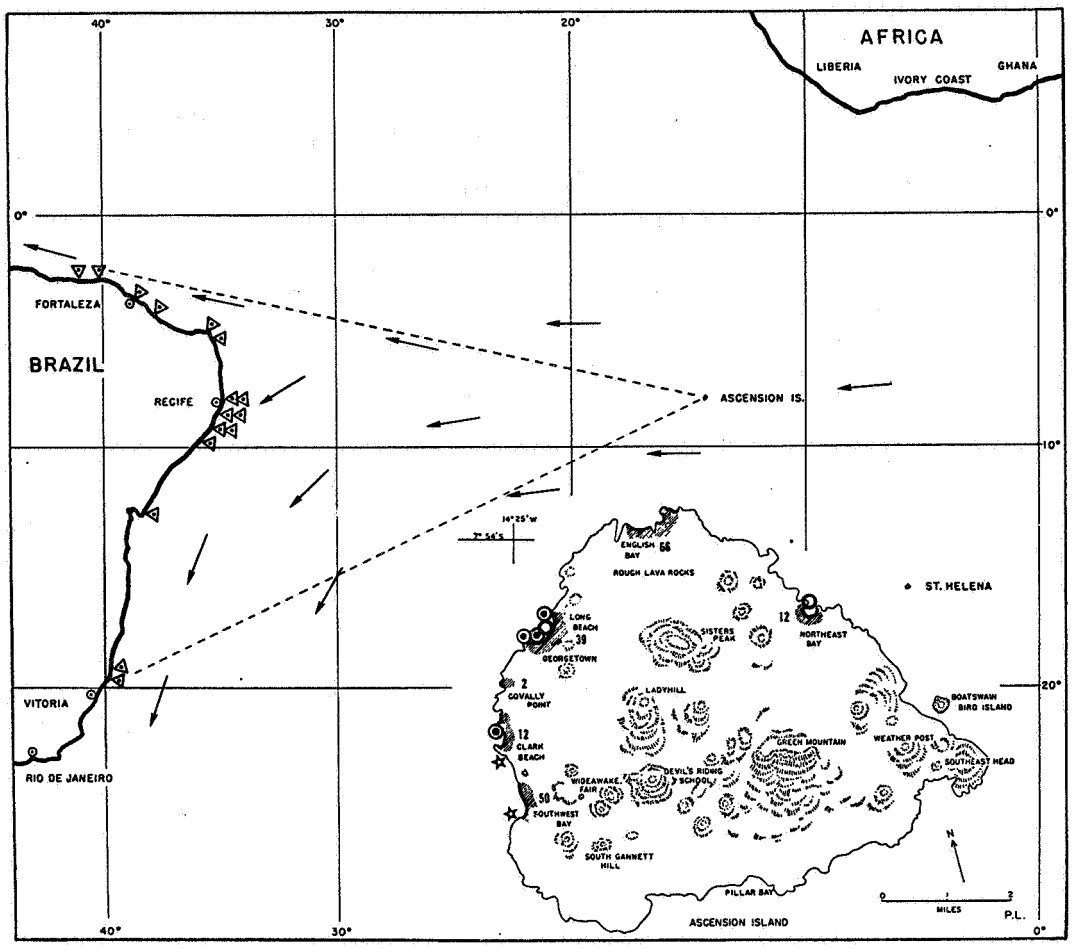


FIGURE 1. Results of four seasons' tagging at Ascension Island, where 660 mature female green turtles have been tagged. Triangles represent recoveries along Brazil coast. Hollow circles show recoveries of turtles that had been tagged and returned to nest after 2 years' absence. Circles with dots show turtles that were tagged at Ascension and returned to nest after 3 years' absence, presumably in Brazil. Stars represent turtles that returned to nest 4 years after they were tagged and presumably after having made two round trips to Brazil. Turtles recovered at Ascension had gone back to original nesting sites. Arrows suggest current trends.

involved in the ecological geography of at least some populations of *Chelonia*, both in the transporting of the hatchlings into their presumably pelagic first-year habitat, and as a vehicle for the olfactory guidance cues that may be used by the migrating adults in their travel to the breeding ground. When Koch, Carr and Ehrenfeld (ref. 1) suggested a dual olfaction-and-Sun-compass mechanism to explain the ability of Brazilian green turtles to locate their Ascension Island breeding ground (fig. 1), they considered this a special case in which the westward flow of the South Equatorial Current affords a unique sensory

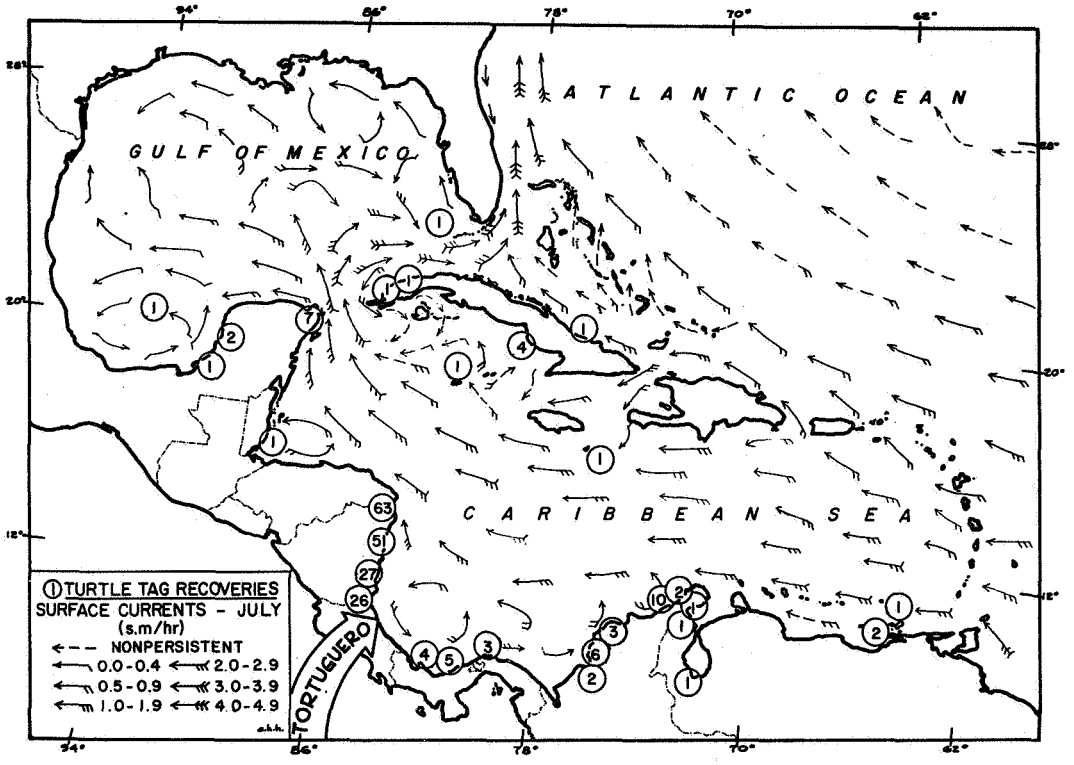


FIGURE 2. Distribution of recoveries of mature female green turtles tagged at Tortuguero, Costa Rica, 1955–1969. Circled figures indicate numbers of recoveries. Arrows show general trend and strength of currents in the Western Caribbean for July (data from Wüst, ref. 13), the arrival time of the nesting schools at Tortuguero.

link between the island rookery and the resident grounds along the coast of Brazil. The relative shallowness of the surface current was seen as an additional special advantage that would not only limit diffusion of any dissolved substances given off by the island, but also might allow the migrants to dive below the thermal discontinuity for rest. This would not only avoid the setbacks that would be imposed by rest in the contrary surface current, but also would allow the sensory recuperation considered necessary for prolonged olfactory appraisal of changes in strength of the Ascension emanation.

That suggestion was made before the authors were aware of the existence and apparently widespread occurrence of equatorial counter currents. Since the first subsurface equatorial current was detected by Buchanan (refs. 6 and 7) in the Central Atlantic, there has been growing evidence (refs. 8 to 11) that equatorial counter currents flow beneath the global surface currents of the Atlantic, Pacific, and Indian oceans. The accumulating data on these currents not only reinforce the possibility that dissolved chemicals may serve as long-range beacons guiding the migration of South Atlantic *Chelonia* but also suggest that currents may be widely involved in molding the ecological geography of sea turtles. Although information on seasonal variations in the depth and velocity of the

counter-currents is limited, there are indications that they flow at depths within the diving range of a green turtle. Jones (ref. 12) even found that the Pacific Equatorial Undercurrent sometimes rises to the surface of the sea. The counter-currents might therefore serve both as an asylum for olfactory recuperation and as a means of continuing progress in the general direction of the goal during periods of rest.

It has only recently occurred to the author that horizontally juxtaposed surface currents might afford some of the same advantages for long-range migratory guidance postulated for the vertically juxtaposed equatorial currents. Data from drift-bottle releases on the Caribbean coast of Costa Rica, and other information on local currents there, suggest that a modification of the chemoreceptive piloting theory might be equally applicable to this migration, in which the goal is a mainland beach.

As part of our search for the developmental stations of first-year green turtles, which disappear for about a year after leaving their nests at Tortuguero, Costa Rica, a drift bottle project was initiated there in 1963 and has been continued each season since. The initial aim was to provide clues in the search for the hatchling habitat, on the assumption that the little turtles are pelagic, and essentially planktonic—unable to influence their displacement materially by their own locomotion. All bottles were dropped from airplanes during October, the time of peak frequency of hatchling emergence. A total of 5351 bottles were released, at points 1 to 19 km off the northeast end of the nesting beach. There have been 175 recoveries distributed as shown in figure 3.

Generalized diagrams of current trends off Costa Rica, such as that of Wüst (ref. 13, see fig. 3), suggest that bottles put out off Tortuguero beach might be recovered either to the south or to the north of the release point, depending on whether they lodged in the north-trending Equatorial Current or in a south-trending inshore current that is perhaps a segment of the gyre shown in Wüst's chart. Our 15 years' observations at Tortuguero have shown that, throughout the turtle season, floating islands and rafts of water hyacinths from the rivermouths of the region move consistently southward when close enough to shore to be seen from the beach. The speed and width of the inshore current appear to vary both seasonally and sporadically, and occasionally the flow may even turn northward for a while. Nevertheless, both Wüst's data and observed movements of flotsam show that a bouyant object dropped off the turtle beach might go either northward or southward, depending upon the distance offshore of the point of release, and on the width of the longshore current at the time. That this hydrologic pattern is involved in the ecologic geography of the Tortuguero nesting colony seems likely.

In 1962 (ref. 14) Carr and Hirth called attention to the consonance of the migration pattern of the green turtle colony of Ascension Island in the South Atlantic (fig. 1) with those of other marine species in which mature animals travel upstream in a current to a breeding place from which the weak, naive young are then passively carried downstream by the same current. Anadromy, in which marine animals travel up rivers to breed, is a special variant of this pattern. In the case of the Ascension Island green turtles, none of the tens of thousands of hatchlings that emerge there each season are ever seen anywhere near the island after the hatching season is over; nor, by logic, should they be. The narrow shelf around the oceanic island offers neither food, nor shelter from predation by fishes and birds. The conclusion is, thus, that the hatchlings swim offshore a

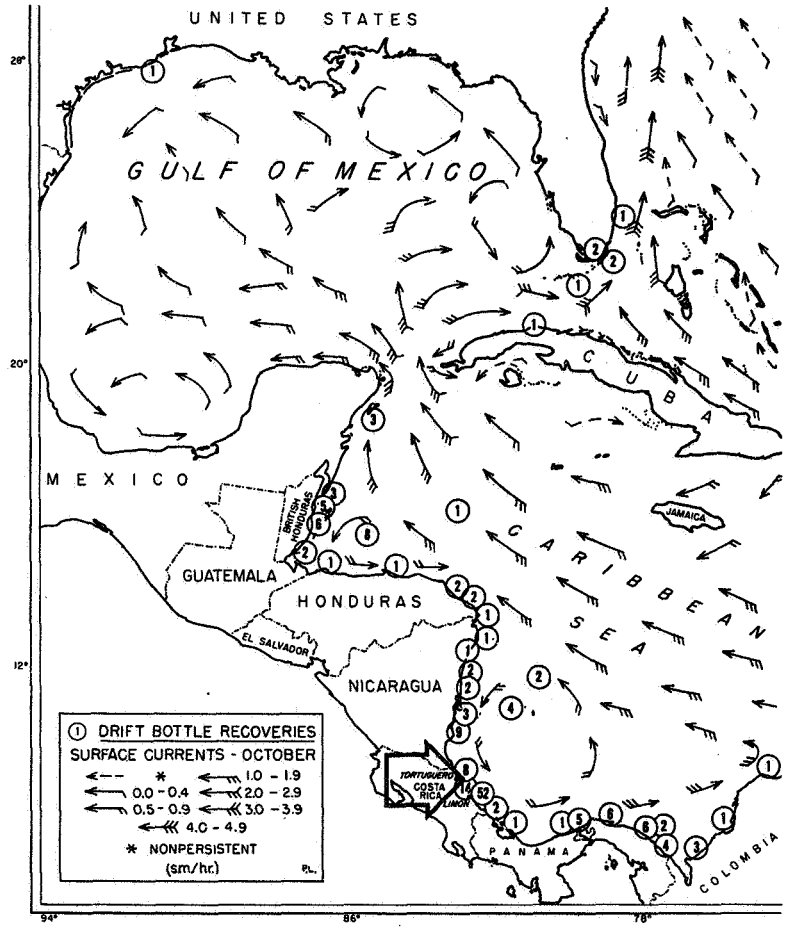


FIGURE 3. Recoveries of drift bottles (circles) released at Tortuguero, 1963 through 1969, in October, the time when most of the hatchlings enter the sea at the Tortuguero nesting ground. Arrows indicate trend and strength of currents for October (data from Wüst, ref. 13).

short way and are picked up and carried away by the Equatorial Current, which at that place and season flows westward at a speed of about one knot.

Where the current takes them is a part of the "lost-year" puzzle. It is of interest, however, that at both Ascension and Tortuguero the only overt move required of a hatchling, in order to initiate its passive dispersal to distant places, would be strong, oriented locomotion immediately after it enters the sea, to move itself beyond the hazards of the surf and shore-water and into a medium of long-range transport.

Appropriate responses are innate in hatchlings. The tendency of young sea turtles of all kinds to swim furiously against the walls of a container has been repeatedly noted. Under natural conditions this swim-frenzy is coincident with a strong motivation to move away from the shore; and this, in turn, seems to be an extrapolation of the

directional sense that guides young turtles across the beach from the nest to the sea on a course normal to the surf-line. Observations of hatchlings immediately after they have passed through the surf suggest that they continue to move directly away from land for some time. That this oriented swimming could disperse them into their unknown but clearly remote first-year habitat, or series of habitats, seems unlikely. There can be little doubt that currents are the main long-range dispersal agent and that the swim-frenzy is merely a mechanism to get the young turtles away from the coast and into the current. In any evaluation of the probability that the migrating adults find chemical cues in the same current, this advantage to the hatchling should be considered.

The possibility that olfaction is a component of the guidance mechanism seems further reinforced when Ascension Island and Tortuguero are compared, with respect to their relation to the places of origin of the colonies that nest there and to the current systems of the areas. As figure 1 shows, Ascension Island receives migrants from both north and south of the bulge of Brazil. Results of the 15-year tagging program at Tortuguero show that there, too, females that nest each year, between July and October, comprise a northern contingent, mainly from the Miskito Cays off Nicaragua, with smaller groups derived from more distant resident grounds as far away as Cuba and Florida; and a southern element, from Panama, Colombia and Venezuela (fig. 3).

It seems unlikely that any form of visible-landmark piloting could be the guidance mechanism for any except the last stages of the periodic, mass arrivals of green turtles at Tortuguero and appears reasonable that chemoreception may be involved in this case, also, even though the goal is a section of mainland shore. From both Ascension and Tortuguero, dissolved marker chemicals might be carried northward for great distances by the Equatorial Current and its branches. Moreover, Brazilian turtles from home grounds south of the bulge could be led into the South Equatorial Current by its branch, the southtrending Brazil Current. As our drift bottle returns show, the inshore current at Tortuguero could carry chemical cues to resident colonies on pastures as far south as Panama and Colombia. If the latter made their breeding migration in coastal waters, they could overcome sensory fatigue, if this actually is necessary, by moving periodically out of the longshore current and into offshore water, just as the Ascension migrants are assumed to move vertically into the subequatorial counter current.

It at first seems another striking point of agreement in the Ascension and Tortuguero patterns that hatchlings entering the sea in either place might be transported directly to the parental residence grounds. This suggests that the same current that guides the migrating adult transports the offspring back to the home territory of the parents. Such a possibility, however, would be based on an assumption that hatchlings emerge with a genetically controlled racial tendency to control the direction of their passive transportation by varying the duration of their swimming toward the open sea. That is, Colombian hatchlings might relax their swim frenzy only a few hundred meters off shore, and so be swept southward, while Mexican hatchlings would continue to swim seaward long enough to be picked up by the northerly Equatorial Current. In order for such dichotomy to evolve as an adaptation, however, segregation of mating pairs at the breeding ground would have to be ensured, with Colombian and Panamaian males mating only with Colombian and Panamaian females, and so on. There is no evidence, either positive or negative, that

such selection occurs. In any case, however, the idea of bipolarity in the dispersal of the hatchlings may be a red herring, because young green turtles are never found anywhere near the parental residence pastures. The least objectionable assumption to explain their lost year appears to be that they take asylum in sargasso rafts in open ocean. Nevertheless, it must be significant that at both Tortuguero and Ascension hatchlings have quick access to currents that could serve as the agent of their hidden developmental travel.

Thus, in the two best-known migration patterns of marine turtles—those of the Ascension Island and Tortuguero colonies—the trends of regional currents could aid both the dispersal of the young and the navigation of the migrating adult returning to her hatching place, with only a chemoreceptive imprint and a Sun-compass sense to guide her. That conditions at both a mainland nesting beach and a small oceanic island afford this dual advantage suggests that the pattern may be a widespread one, and this possibility seems strengthened by recent oceanographic data. Further testing of the idea may reveal that, other things being equal, a good nesting beach, in the eyes of *Chelonia*, is one that lies near a current system capable of providing (1) olfactory guidance for the nesting migrations and (2) appropriate transportation for the newly hatched young.

THE ROLE OF TRACKING AND TELEMETRY

The most important obstacle to investigation of this and other aspects of the ecology and migrations of the five genera of marine turtles is the difficulty of keeping in touch with them in the open sea. Most of what has been learned of sea turtle ecology has come from tagging-and-recovery data, and while a good deal can be deducted from such point-to-point contacts, the data leave fundamental aspects of the life cycle completely obscure. Although all the genera appear to be at least partly migratory, their routes of travel have in no case been adequately traced.

Caretta is sometimes sighted on the high seas and is also seen in estuaries or even in little creeks in salt marsh. *Chelonia*, being herbivorous, comes under observation by turtlers on its shallow-water pasture grounds. Divers find hawksbills about submerged rocks and reefs. The Atlantic ridley is accidentally taken off the coasts of Florida by shrimp trawlers or in green turtle nets, and seamen and hide hunters intercept schools of Pacific ridleys in deep waters off Mexico and Central America. Leatherbacks are frequently harpooned by fishermen off New England and Nova Scotia and in the Sea of Japan. Such sightings as these, however, are usually so fleeting that little is learned from them. Often even a firm identification is impossible. For instance, the Airborne Radiation Thermometer Program of the U. S. Coast Guard has compiled a massive record of sightings of sea turtles along the inner edge of the Gulf Stream; and while the turtles recorded are no doubt mostly loggerheads, the admixture of other species cannot always be detected, and this defect obviously lowers the value of the data.

During the past 8 years, one aspect of the program of sea turtle research at the University of Florida has been a series of attempts to track sea turtles in their local and long-range travel. Although this work has never advanced beyond the equipment-testing stage, a few partly successful tracking runs have been made. The desultory data that have accumulated—some of which have appeared in previous publications—are plotted in figures 4 to 10. The tests were carried out in Florida, Costa Rica, and in the South Atlantic off

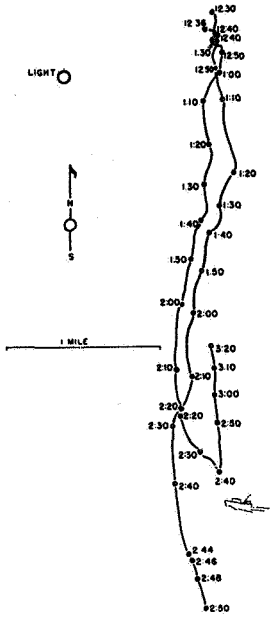


FIGURE 4. Travel of two female loggerhead turtles taken when emerging to nest on Atlantic coast of Florida and released, out of sight of land, directly across the peninsula in Gulf of Mexico (ref. 15).

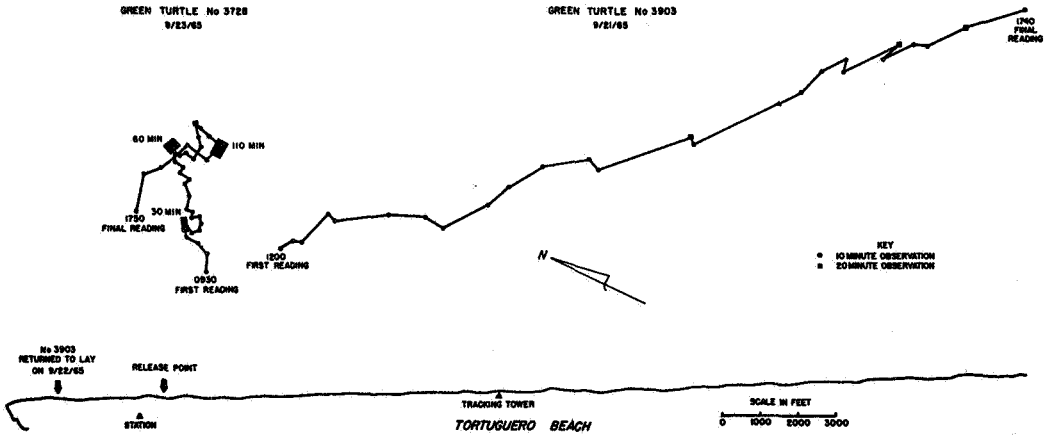


FIGURE 5. Plots of movements of two female green turtles visually tracked off Tortuguero, Costa Rica. Tracking alidades were located at the Station and tracking tower on the beach. One turtle (no. 3728) had been allowed to nest before being fitted with a tow-float and helium balloon and released off the nesting beach. The other (no. 3903) was rigged and released before nesting. No. 3728 had evidently not finished her suite of renestings for the season. The motivation of the purposeful and seemingly well-oriented course of no. 3903 is not apparent, since she returned to the beach the following night and nested at point indicated (ref. 5).

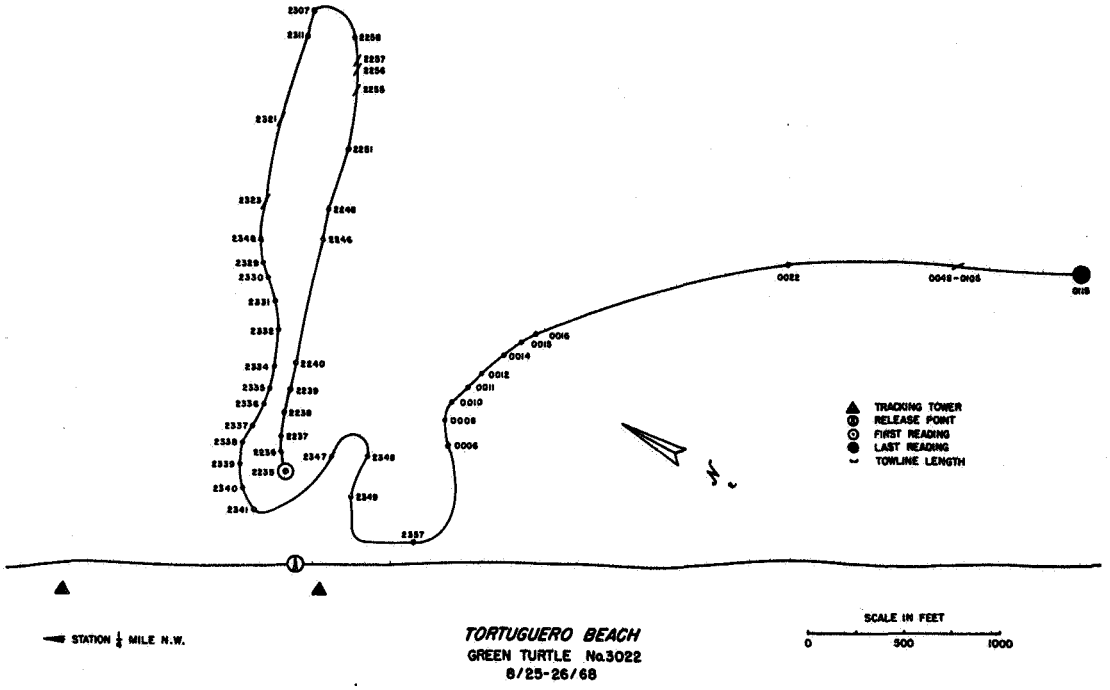


FIGURE 6. Plot of movements of mature female turtle visually tracked at night at Tortuguero, Costa Rica. The turtle was taken just before nesting and rigged with a tow-float bearing a single flashlight bulb at top of 1-meter mast. Bearings were recorded by alidades located at two tracking towers a half-mile apart on the fore-shore.

Ascension Island. In an effort to learn where a female sea turtle goes and what she does during the 12-to-14 day intervals between her nesting emergencies at the rookery, tow-floats and helium balloons have been used in daytime tracking (figs. 5 and 8) and lighted floats at night (figs. 6 and 7).

There has also been a series of largely unsuccessful efforts at tracking by radio. The first of these were made with transmitters fastened to the carapace of the travelling turtle. Of various defects in this system, the most fundamental was the limitation of the transmission period to the time when the turtle emerged to breath and exposed the whip antenna that rose from its back. More recently, in collaboration with Sensory Systems Laboratory, transmitters, and in some cases sensors capable of telemetering heading and velocity, have been installed in floats and attached to experimental turtles by long lines. Although both green turtles and loggerheads have shown themselves to be amenable to such manipulation, electronic troubles have plagued these efforts too.

One of various applications of long-range tracking techniques to the study of sea-turtle natural history is in the gathering of information with which to test navigation theories. To theorize about the pathfinding mechanisms used by an animal when the paths it takes are unknown seems unpromising, if not simple-minded, when the process involved is as clearly complex as this one is. The slow

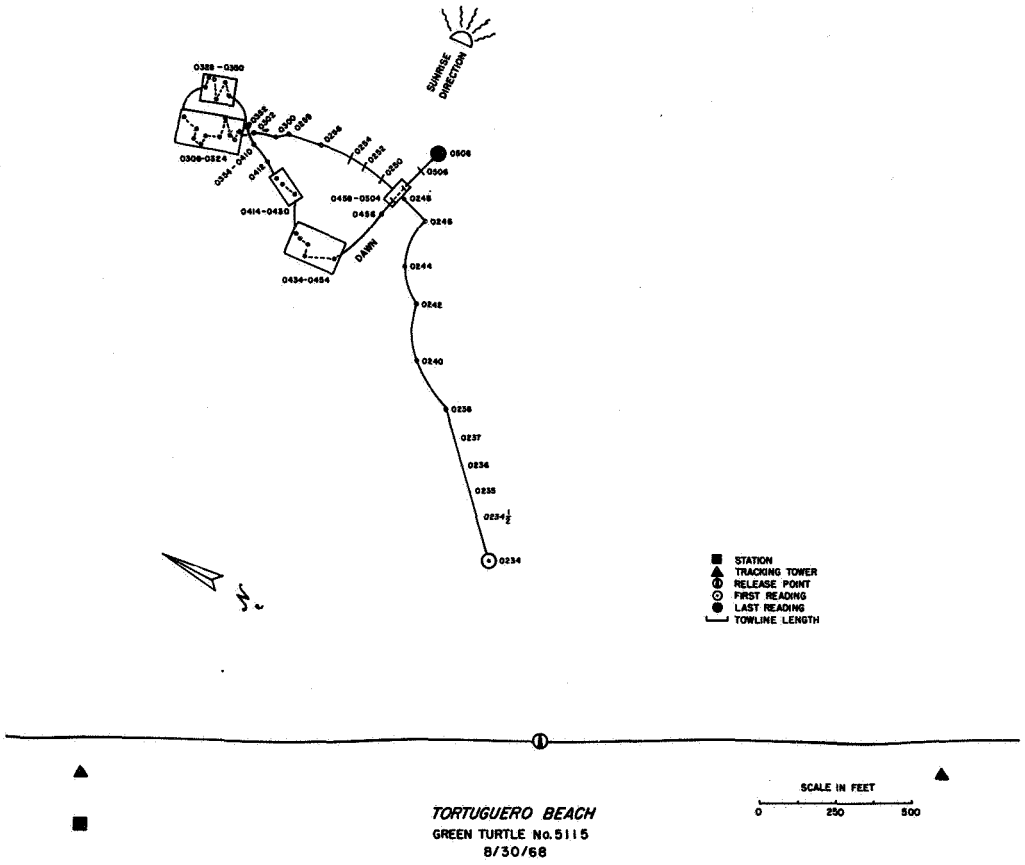


FIGURE 7. ***Movements of mature female green turtle visually tracked at night at Tortuguero, Costa Rica, after completing nesting emergence. Turtle was rigged with illuminated tow-float, and bearings were taken with alidades located at tracking towers half-mile apart on the beach. Sudden resumption of activity at the moment sun showed above the horizon, after the long period of relative quiescence, was striking.***

progress of animal navigation theory since its brief period of initial progress seems mainly attributable to the difficulty of tracking animals through significant segments of their long-range journeys in, on, or over the open sea.

The ideal is to trace whole migratory journeys in detail. Much can be learned from appropriate sample segments, however. Figure 9 suggests five ways in which such samples bear upon three fundamental questions to be asked about the travel path of an animal in open-ocean migration. These are (1) whether the travel is oriented or random, (2) whether the direction taken is a preferred direction, and (3) whether the course is, in the view of the observer, an appropriate one.

Test A in figure 9 involves one experimental animal and a single tracking run. The aim is to test for any tendency to maintain a nonrandom (rectilinear, curvilinear, cyclical) course. Obviously the tests gain significance

as the distance is increased. It should be stressed that in this trial the experimenter is not concerned with either the appropriateness of the course chosen or the frequency of a given guidance capacity in a population—only with the degree to which an individual migrant adheres to a nonrandom course. Thus the straight line is not drawn between end points of the segment but is put in as a trend-line to show mean performance. In trials B through E, on the contrary, the line that serves as the criterion for direction-holding capacity is the mean vector, drawn as shown, between endpoints in the timed travel-path.

In test B a single animal is used in repeated tracking runs. Sample size is augmented by increasing the number of trials. Such a test would logically be made after positive results had been obtained in experiment A, with the aim of determining whether the capacity for nonrandom travel is coupled with a tendency to choose the same direction in repeated trial runs. It is thus a test for both nonrandomness of travel and direction preference but not one for "goal" sense. In experiment C various animals are used in tests like those of B to learn whether a preferred direction trend is an individual or racial attribute. Sample size is increased by increasing the number of individuals.

A specific goal drive is assumed in test D. A turtle of the Ascension Island nesting colony, for example, is taken as she comes ashore to nest after a migratory journey from Brazil, carried back out the assumed line of her migratory travel, and released. The aim is to determine the success with which the migrant was able to repeat that segment of the Ascension travel. The test is designed to answer the question: How closely does the mean vector conform to the true course to the "goal" as assumed by the experimenter? Sample-size would be increased by repeating

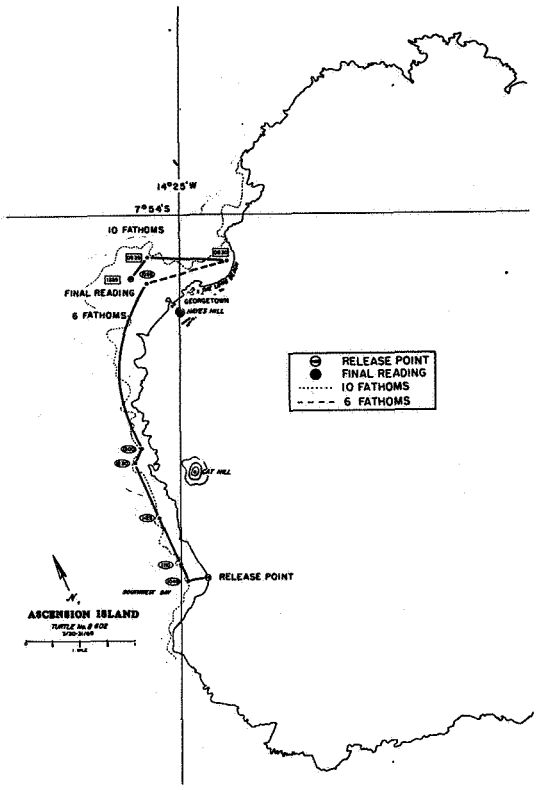


FIGURE 8. Movements of female green turtle (no. B 602), visually tracked after release at Southwest Bay, Ascension Island. Turtle had nested the night before. Close approach to the surf on Long Beach Cove was unexpected and unexplained.

runs. In experiment E, data from various goal-motivated animals, tested in the same area as that used in D would show how prevalent the goal-trend is in a *population*—that is, how widespread the tendency and capacity to hold a particular course are in the particular breeding colony from which the sample was taken.

During March 1969 an effort was made to carry out surface-to-surface tracking and telemetry using female Ascension Island green turtles displaced before completing their nesting venture. The plan involved four experimental animals. The transmitters to be used

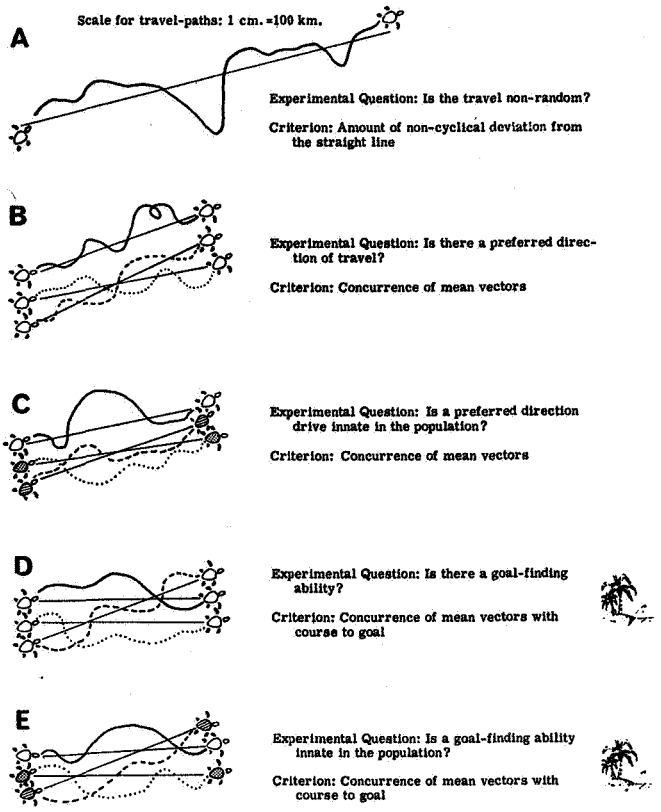
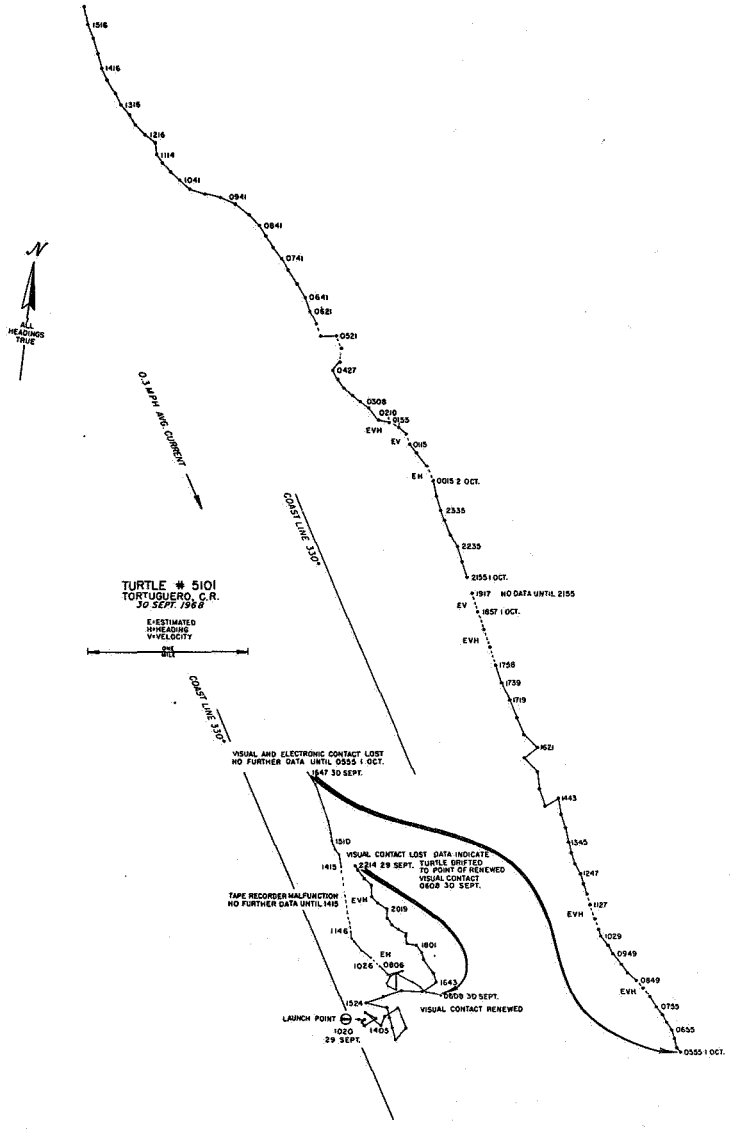


FIGURE 9. Five kinds of tracking experiments involving marine turtles, motivated to travel, and released in open ocean.

had an expected range of 480 km and a power-life of 2 weeks. The system had been given preliminary tests at Tortuguero, with results shown in figure 10. The equipment used is described by Baldwin.[1]

The assumption to be tested was that the Brazilian green turtle population is guided in its 1920-km (minimum) journey to the Ascension Island nesting ground by a dual orientation process in which olfactory appraisal of the north-south gradient in an emanation stream down the South Equatorial Current from Ascension keeps the migrants in the latitude of the island, while a Sun-compass sense maintains the necessary easterly course. The plan of the experiment was to release four turtles at a distance of 160 km from the island; two of them downstream in the current, and two others across the current to the north. The equipment was designed to telemeter magnetic heading and velocity. If the assumed navigation mechanism was correct, the downstream subjects might have been expected to return to the island, perhaps on a zig-zag course corresponding to a gradient appraisal regimen. If the turtles put out

[1] BALDWIN, HOWARD A.: Long-range radio Tracking of Turtles (in press).



FIGURES 10. Telemetered course of green turtle no. 5101, released at Tortuguero, Costa Rica, after nesting there the night before. Because of fluctuations of inshore currents at release site, it is unknown how closely the course plotted from the telemetered headings and velocities correspond to actual travel pattern; however, mean vector for travel headings closely approaches a true course to Miskito Cays, one of the principal resident grounds of Caribbean *Chelonia* (see fig. 2).

across the current had oriented successfully, the theory under test would automatically have been discredited.

Damage to equipment in travel to the island eliminated three of the experiments and curtailed the fourth after about 2 hr.

Heading data from the single aborted run are shown in figure 11. These headings were taken by an animal orienting in open ocean where it was presumably isolated from all solid landmarks and, because of its position in the current, obviously not in olfactory contact with the island. Although nothing of significance is revealed by the degree of consonance of the course with the true course to Ascension, the travel of the subject was quite obviously non-random.

If this experiment had proceeded as planned, with continuous heading data coming in from both downstream and across-stream subjects, results would have permitted evaluation of navigation theories in various ways. If a Sun compass had actually been in use, for example, orientation should have failed at sunset. If the subject had slept at the surface, it would have been borne westward by the surface current during the night; if it had dived beneath the thermocline to rest, it would have remained stationary or been carried in an easterly direction by the counter-current. In neither case, however, would there have been evidence of orientation in the night-time heading-data. If all turtles released had returned successfully on direct courses, bicoordinate celestial navigation, or some equally complex mechanism, would have had to be reconsidered.

In spite of this setback in the effort to track the Ascension Island migrants, the colony remains a promising source of data for animal navigation theory. The relatively steady ocean current, moving directly along a parallel of latitude from the breeding island to the nearest projection of the mainland residence ground, suggests chemoreception as a guidance cue. Evolutionary feasibility favors the idea: back-tracking an imprinted smell-stream to a tiny mid-ocean island seems a more evolvable adaptation than the Earth-map and star-almanac a migrant would need

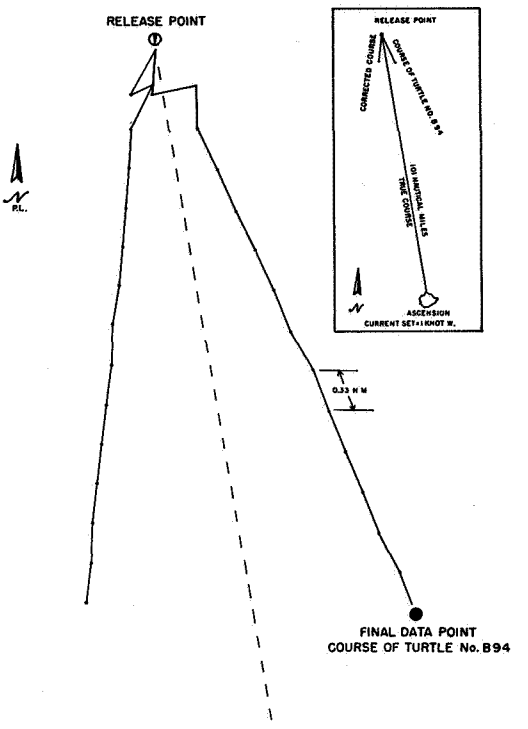


FIGURE 11. Course dead-reckoned from 13 headings telemetered by green turtle no. 94, rigged with tow-float after being interrupted in nesting at Ascension Island and released 101 nautical miles NW of the island (06°15'S, 14°41'W). Velocity assumed was 0.33 nautical miles per duty-cycle interval. Course corrected for current-set is the line at left.

in order to correct offcourse aberrations by celestial bicoordinate navigation. The weaknesses of the chemoreception theory are our ignorance of the migratory paths, the dearth of data on the sensory acuity of the species, and the regular mass arrivals at Ascension of 10 kinds of migratory sea-birds that surely have not smelled their way out there.

ACKNOWLEDGMENT

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DISCUSSION

QUESTION: Do you have plans, if the telemetry system works, for placing the turtles in different directions from the island?

CARR: Yes. The need is for a well-designed experiment in which a number of animals are set out at sites suggested as strategic by oceanographic and statistical considerations.

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Homing Orientation in Salamanders: A Mechanism Involving Chemical Cues

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University of Wisconsin

THE SALAMANDER *Plethodon jordani* possesses a well-developed homing response that is both highly oriented and direction-independent (refs. 1 and 2). Some individuals have homed following 300-m displacement, a distance 20 times the greatest linear dimension of any home area recorded. The objective of this paper is to report on a series of experiments concerning the senses and cues used by *P. jordani* during homing orientation.

Information on sensory involvement in caudate homing orientation has been obtained mainly by manipulating the experimental subject, either by sensory impairment, conditioning procedures, or rhythm alterations. By such techniques, olfaction (refs. 1, 3 and 4) or photoreception (ref. 5), or both (ref. 6), have been generally shown to be necessary senses. One species of newt (*Taricha rivularis*) homes readily following extirpation of the eyes (ref. 7) but fails to home following severence of the olfactory nerves (ref. 4). However, homing is completed in some cases when the olfactory nerves have regenerated. Studies with a formalin perfusion technique have also shown olfaction to be important to accurate homing orientation in this species (ref. 3). Another newt (*Taricha granulosa*) has been shown to use light cues for spatial orientation under laboratory and field conditions (refs. 5 and 6). Extraoptic photoreception (near the diencephalon) has been demonstrated for the salamander *Plethodon glutinosus* (ref. 8). A similarly located system in a frog (*Acris gryllus*) can even receive directional information to be used in homing orientation (ref. 9). Senses involving other than photoreception and chemoreception have received little attention in caudate homing studies. One exception is Twitty's work which showed that substrate contours were not important for initial homeward orientation in *Taricha rivularis* (ref. 7).

Techniques involving the manipulation of natural cues, which are similar to those methods used by Kramer with starlings (ref. 10), have not been employed in caudate investigations. One advantage of these methods is that the experimental animal can be left in a relatively normal biological state and be less subject to possible experimental trauma. Such

techniques should be used to supplement the results obtained from sensory impairment studies, particularly when diminished response patterns following sensory impairment are given as evidence of the importance of the sense to the response in question. Both sensory impairment and cue manipulative techniques are used in the following investigation.

GENERAL METHODS

Plethodon jordani Blatchley are terrestrial salamanders of the southern Appalachian highlands that live at high elevations in moist woodland habitats away from aquatic media. They are non-migratory and quite sedentary. Being lungless and depending largely on skin moisture for cutaneous gas exchange, they are vulnerable to dehydration and anoxia. The species is active on the forest floor at night, a time of greater relative humidity, and spends the day under cover usually in burrow systems. An average adult has a total length of 115 mm and a width of 10 mm.

Observations and Subject Handling

Details of the general procedures may be obtained elsewhere (refs. 1 and 2). Briefly, all observations were conducted at night, particularly between 2100 and 2400 hr, the period of greatest subject activity. Each animal when hand captured was uniquely marked by toe-clipping and checked for sex and size. If displaced, the salamanders were denied visual cues. No anaesthesia was used; the animals were retained for typically less than 30 min. Both marking-recapture and radioactive ^{182}Ta-tagging procedures were used to record the animals' movements. Displacements were made usually of 30 m, a distance twice the greatest home-range dimension yet recorded. This distance reduced the time required for displacement and the time required for relocating the salamanders that were momentarily lost, while still satisfying the requirement of displacement into unfamiliar areas. Almost invariably, displaced salamanders either remained in the vicinity of the release point (within 12 m) or returned close to the initial capture position (within 8 m). The latter animals were considered to have homed. Throughout the studies, wind directions were frequently measured. On a given night wind conditions were usually such that, at one time or another, breezes from most all directions were recorded.

Analytical Procedures

Nonparametric statistics were used throughout, specifically the Mann-Whitney U test and the Chi Square test on 2×2 contingency distributions, where appropriate (ref. 11). Rejection of the null hypothesis was based on the .05 level of significance. Rejection at lower significance levels are so indicated.

SENSORY IMPAIRMENT

Because it was suggested from other experimental work that vision and olfaction may be quite important to homing, these senses were selected for impairment studies. With certain provisions, the impairment of these senses should indicate their relative importance to homing in terms of their necessity. The provisions are that suitable controls for trauma or other subtle effects are instituted and that sensory impairment does not severely disrupt normal locomotion through the environment.

Methods

Impairment procedures were performed in the field just prior to displacement. Salamanders were blinded by extirpating the eyes.

The olfactory nerves were severed by two methods: In the first, two small incisions were made through the skin and cartilage of the cranium anterior to the brain case. A sharp probe was then inserted into the incisions and moved through the nerve axes. Details of this technique have been reported (ref. 1). Sham operations consisted of only the initial incisions.

In the second method, the nerves were severed by making incisions dorsally through the roof of the mouth using delicate, sharp-pointed surgical scissors. For each nerve, one tip of the scissors was placed into the laterally situated internal naris, and the other was inserted adjacent to the medial nasal septum on the same side. A quick snip was then made which severed the cartilage, the dorsal and ventral divergences of the olfactory nerve, and the contiguous tissue in the same nasal area. The cartilage above the nasal chamber was usually left intact, thus reducing the chance of infection through a direct external wound. Also, the mucous glands and ducts between the cartilage and skin on the dorsal surface of the snout were left intact. The second method was used in place of the first in 1970 after it became apparent that occasionally the olfactory nerves, instead of being severed by the transverse movements of the probe, were only displaced temporarily to one side. Also the second method was more consistent from one operation to the next due to the local anatomical references. Both unilateral and bilateral anosmic operations were performed.

One additional sensory impairment was attempted. The nasolabial grooves, single superficial furrows from the upper lip margin to the external naris on each side, were shaved off by a slender scalpel in an attempt to disrupt a possible avenue of substrate chemoreception (ref. 12).

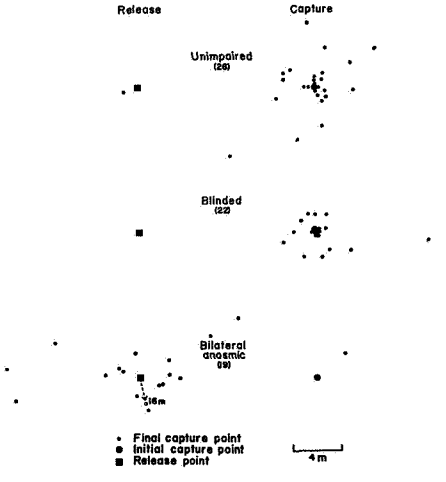

FIGURE 1. Final points of capture of all sensory impaired and unimpaired salamanders displaced 15 m in 1965. Number in parentheses indicates number of adults of each treatment group represented. Actual displacements in each of four directions are combined and included as a single direction. After Madison, 1969.

Results and Discussion

A preliminary study involving marking-recapture methods was conducted in 1965. Unimpaired, blinded, and bilateral anosmic salamanders were displaced 15 m in various directions. The results (ref. 1) indicated that the olfactory sense may have been necessary for successful homing (fig. 1). Blinded animals homed without apparent difficulty.

A second displacement series was conducted during the summer of 1969. Thirty each of four treatment groups (bilateral anosmics, sham anosmics, blinded without the nasolabial grooves, unimpaired) were displaced 30 m. A fifth treatment group of 30 sensory unimpaired animals were left at the point of initial capture as displacement controls. Adult salamanders were selected at random for each treatment. Of all the animals recaptured during 1969, the relative number of anosmics that homed was significantly less

TABLE 1.—*Comparison of Number of Salamanders Recaptured and Homed for Various Treatment Groups During Summer of 1969 (31 night searches) and Spring of 1970 (3 night searches). UC, unimpaired control; UD, unimpaired displacement; BN, blinded and without the nasolabial grooves; SA, sham anosmic; BA, bilateral anosmic.*

Treatment group	Number marked (1969)	Number recaptured (1969)	Number homed (1969)	Number recaptured (1970) [a]	Additional home (1970)
UC	30	20	.....	2(0)	.....
UD	30	23	20	7(1)	1
BN	30	27	21	3(0)	0
SA	30	20	17	3(0)	0
BA	30	12	2	4(1)	4

[a] Number in parentheses indicates animals recaptured for the first time.

than the relative number of each of the other treatment groups that homed ($p<.001$) (table 1). The fact that the sham anosmics homed in similar percentages to the unimpaired treatments would seem to indicate that trauma was not primarily responsible for the poorer anosmic returns. In any event olfaction again seemed to be important for the normal homing response.

In the following year (1970) four "anosmic" salamanders were recovered at home for the first time, suggesting the occurrence of homing after regeneration of the olfactory nerves, as has been previously recorded for another salamander species (ref. 4). One of the anosmic *P. jordani* was retained to check on the condition of the olfactory nerves. Both nerves were found intact.

To measure the course and timing differences in the homing response due to anosmia, a third displacement series was conducted during August 1969. Eight bilateral anosmic (method 1) and 24 unimpaired salamanders were tagged with ^{182}Ta, displaced 22 to 60 m, and tracked with scintillation equipment. The details of the tracks of the unimpaired salamanders have been reported (ref. 2). Significantly fewer anosmic salamanders homed (4 of 8) than did unimpaired animals (23 of 24) ($p<.01$). In addition, the total homing times (*THT*, the time from release to arrival back home) and the return trip times (*RTT*, the actual time taken to travel the distance home once directed movement was initiated) of the bilateral anosmic animals were significantly greater than those of the unimpaired salamanders. The median *THT* (20.8 hr) and *RTT* (2.8 hr) values for the unimpaired animals can be compared to the individual values recorded for the anosmics (table 2, 1969). Finally the courses of the anosmics that did home seemed to be more irregular (fig. 2).

A fourth set of impairment displacements was conducted in the spring of 1970 to see what effect more thorough olfactory impairment (method 2) and unilateral anosmia (right side only) might have on homing, and to determine if the homing courses of the blinded salamanders differ from those of the unimpaired animals. The unilateral anosmia treatment was added to see if possible traumatic effects of the olfactory operation might delay homing even though intact olfactory tissue was present. Unilateral and bilateral anosmic, blinded, and unimpaired displace-

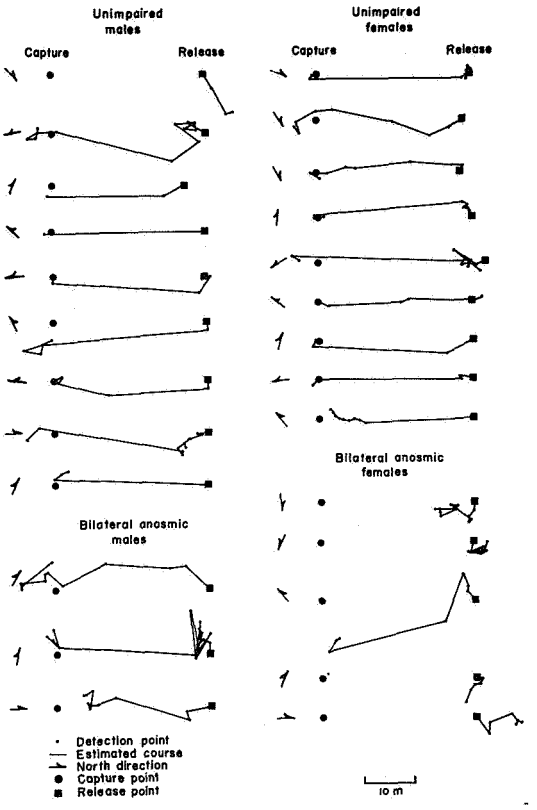

FIGURE 2. Estimated movements of all anosmic and unimpaired salamanders displaced upon initial capture during radioactive tagging study of August 1969.

ments of 24 to 68 m were made in various directions. Except for the different anosmia technique, the same methods and radioactive tracking procedures were used.

The sensory unimpaired salamanders, as in the previous cases, homed more frequently (6 of 8) than did the salamanders with bilateral anosmia (0 of 8) ($p<.01$). The homing performance of the unilateral anosmics (2 of 8) was intermediate to, but not significantly different from, either the bilateral anosmics or the unimpaired treatment groups. The blinded salamanders homed in frequencies (2 of 4) comparable to those of the unimpaired animals. Except for one unimpaired salamander, the homing times in 1970 were similar (table 2). The courses of the salamanders which homed (10 of 28) showed accurate homeward orientation regardless of treatment (fig. 3). Since the positions of these 10 salamanders were determined on a total of 264 of 267 attempts, these courses are not biased to include only those detection points in the home direction. The movements of the 18 salamanders which failed to home were confined to within 12 m of the release point (fig. 4). The positions of these salamanders were determined on all of the 891 attempts.

The poorer homing frequency of the unilateral anosmic treatment group (in comparison with the unimpaired group) could have been due to a reduction of the total olfactory input. This reduction to one-half may simulate the results obtained by displacing unimpaired animals twice as far. The reduced homing frequency is probably not the result of inhibitory effects on movement incurred as a result of the operation. This lack of an inhibitory effect is supported by the similar

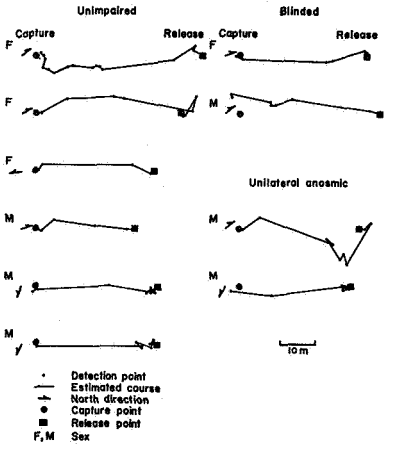

FIGURE 3. Estimated courses of all sensory impaired and unimpaired salamanders that homed during the radioactive tagging study of spring 1970.

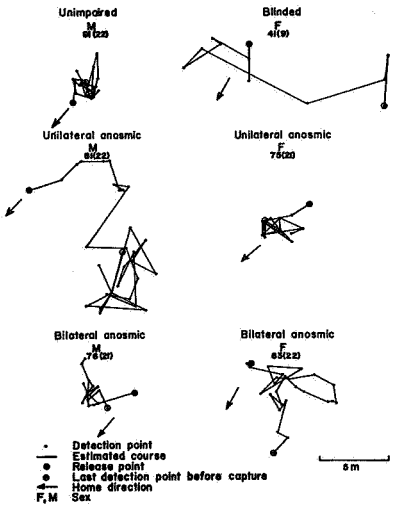

FIGURE 4. Movements of selected sensory impaired and unimpaired salamanders that failed to home during radioactive tagging study of spring 1970. Salamanders shown are those that had been observed for the longest time following displacement, or which, in addition, had demonstrated greatest amount of movement from the release position. Number of detections and days (in parentheses) are shown for each animal. North direction (top of page) is maintained. Multiple detection points at a given location are not indicated.

degree of movement of the salamanders which failed to home.

CUE DISPLACEMENT

Because it was difficult to assess whether all the provisions mentioned in the previous section had been met, the attempt was made to alter the position of the home odors of the displaced salamander instead of altering the capacity of the animal to detect such odors. It was hypothesized that if an animal were displaced to a totally unfamiliar environment, it would be sufficiently motivated to attempt to return home once left alone. In such a situation any familiar trace of odors should elicit oriented movements into the wind in the home direction. Successful luring of the animal in a direction opposite the home direction using the displaced home odors would suggest the use of olfactory cues during homing.

Methods

The odor displacement equipment included an intake and a transport unit (fig. 5). The intake unit consisted of a 10-cm diameter galvanized ventilation pipe which had intake openings along its 1.3 m length and a fan blade and shaft mounted inside at one end. The fan was operated by a belt attached to a 12-v d.c. motor. The latter was housed outside the airstream of the pipe in order to avoid scenting the intake air with odors from the motor. The transport unit consisted of 30 m of 10-cm diameter aluminum ventilator pipe. The two units were connected with a 3-m segment of 10-cm diameter flexible plastic tubing that allowed for placement of the intake over the capture points of the resident animals. The two-unit system was set up adjacent to a stream along an abandoned lumber road that had since grown up with trees. The site along the stream was selected because of the consistent wind direction characteristics there (from upstream, SSW)—a mandatory condition for the experiment.

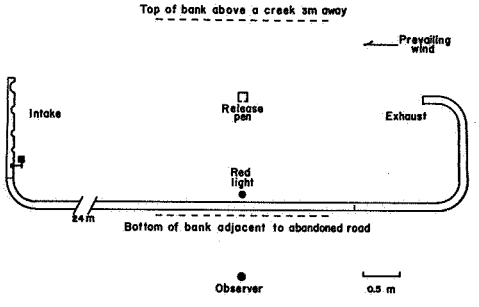

FIGURE 5. Odor displacement apparatus of cue displacement experiment.

TABLE 2.—*Homing Times of ^{182}Ta-Tagged Salamanders Displaced During August 1969 (only those of impaired animals shown) and June 1970. DD, displacement distance; DR, displacement direction; THT, total homing time; RTT, return trip time.*

Sex	DD (m)	DR	THT (night hours)	RTT (night hours)
Bilateral anosmics 1969				
F [a]	30	SE	111.4	58.3
M	30	N	83.9	76.8
M	30	E	113.1	5.2
M	30	NE	44.3	5.2
Unimpaired 1970				
F	42	NE	80.8	42.3
F	36	N	62.9	1.1
F	30	S	47.1	1.8
M	30	SW	44.2	3.3
M	24	N	63.4	2.0
M	30	W	75.3	2.8
Blinded 1970				
F	32	N	60.8	0.9
M	34	NE	31.1	5.9
Unilateral anosmics 1970				
M	30	NE	64.3	2.0
M	28	SW	35.3	2.1

[a] Values not included in statistics due to unreliable time estimates resulting from temporary loss of salamander prior to detection at home.

Local wind speeds varied from trace amounts to gusts of 1.2 m/sec, although typically, and during the observations, the speeds were rather consistent around 0.3 m/sec. The wind speed at the exhaust opening due to the intake fan measured 2.5 m/sec. At the screen release pen, 3 m downwind from the exhaust opening, the speed ranged from 0.1 to 0.3 m/sec.

Salamanders were displaced upwind of their home areas but downwind of the exhaust of the transport unit. Non-resident animals were captured on either side of the road more than 10 m downwind of the intake unit. The resident animals were captured on either side of the road near the intake unit which was in turn placed on the surface litter directly over the capture site of the resident. The displaced salamanders were released into the open side of the small release pen, 27 m upwind from the intake unit and 3 m downwind from the exhaust. A small red light (directed away from the observer and the road bank and toward the release pen and the creek bank) was used for the night observations. The observations began when the salamander voluntarily left the opening of the release pen. Salamanders were scored as moving away from or toward the exhaust relative to a line intersecting the release pen drawn perpendicular to the home-pen-exhaust axis. Movements toward the creek bank or road bank side of the home-pen-exhaust axis were similarly recorded. Seventeen of the 19 salamanders placed in the release pen exited within the alloted time of 10 min. Each of these was continuously observed for at least 10 min or until it went out of sight 2 to 3 m away. Wind direction was monitored continuously throughout the observations 0.5 m above the ground. Although the speed increased with height above the ground, the direction remained the same.

Results and Discussion

Both the resident and non-resident animals were observed to move at random with

respect to directions along the home-pen-exhaust axis (table 3). However, a significant number of salamanders (13 of 16) moved toward the side of the road corresponding to the side on which they were initially captured.

Although these results do not correspond to the expected oriented movements, the results can be accounted for if one accepts the following hypotheses: (1) olfactory cues are relied upon for homing, (2) recognizable home odors were transported successfully in the system above, and (3) a given salamander is able to recognize its position in its home area using only olfactory cues. For example, if a resident's home area was located on the downwind side of the intake, the resident, upon smelling only the odors on that side from the exhaust opening, might well move in a direction which would normally take it to the center of its home area—a direction which at the release pen would be away from the exhaust. By chance, the resident salamanders would be captured with equal frequency in the upwind and downwind halves of their home areas, and thus in the testing situation be expected to move toward the exhaust half the time and away

TABLE 3.—*Direction of Movement of (R) Resident and (NR) Non-Resident Salamanders in the Odor Displacement Study of 1970. Movements (T) Toward or (A) Away from Exhaust Are Indicated. Capture Locations at or Movements Toward (CB) Creek Bank or (RB) Road Bank Also Indicated.*

Date	Animal type	Sex	Capture location	Movements	
				Perpendicular to road	Along road axis
May 26	R	M	RB	CB	T
May 26[a]	NR	F	RB	RB	A
May 26	R	F	CB	CB	A
May 26	NR	F	RB	Along axis	T
May 27	NR	M	CB	CB	T
May 27	R	F	CB	CB	A
May 27	NR	M	CB	RB	A
June 7	R	F	RB	RB	T
June 7	NR	M	RB	RB	T
June 7	R	F	RB	RB	T
June 7	NR	M	?	No pen exit	
June 7	R	F	RB	RB	T
June 7	NR	M	?	No pen exit	
June 14	NR	F	CB	CB	T
June 14	R	F	RB	RB	T
June 14	NR	M	RB	RB	Along axis
June 14	R	M	CB	CB	A
June 14	NR	M	CB	CB	T
June 14	R	F	CB	RB	A

[a] Only animal to receive occasional wind gusts from the home direction downstream.

from it the other times. The significant correlation observed perpendicular to the home-pen-exhaust axis agrees with this hypothesis; however, one additional fact is necessary. As revealed from radioactive tagging studies, salamanders along trail-bank situations seldom have home areas which cross the trails (only 4 of 562 position points on 11 adult non-displacement animals have been observed either on or across the bordering trail). This condition exists even though there are no apparent barriers to salamander movements on the trails. Thus by the same explanation presented for movements along the home-pen-exhaust axis, one can account for the movements perpendicular to the axis.

One would expect then that salamanders in other displacement situations would have shown more ambiguity in their movements as a result of detecting occasional whiffs of home odors from different areas of the home range. Such ambiguity was not observed. The one important difference in the odor displacement situation was that home odors were picked up from essentially the same microhabitat that the animal was occupying and transported 30 m without dilution. Thus the movements observed by the resident animals may not have been homing movements, but rather movements associated with minor adjustments of position within or immediately adjacent to the home area.

It is still a possibility, and a simpler hypothesis to propose, that the movements in the home-exhaust axis were random either because the apparatus failed to pick up the essential odor cues, or because home area odors are not used during homing. That the movement was not random as a result of fright or escape behavior is evidenced by the non-random orientation perpendicular to the road. The latter orientation could have been in response to cues obtained from the directionality of the wind or the cooler air near the stream, both of which were similar to conditions at home.

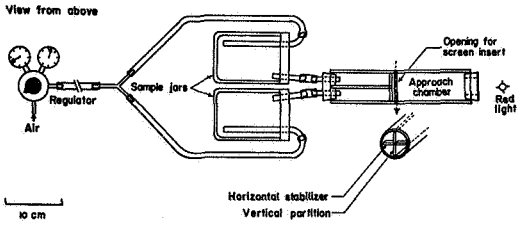

FIGURE 6. Olfactometer apparatus of cue identification experiment.

CUE IDENTIFICATION

The possibility of a salamander recognizing its own position relative to a mosaic of site specific odors or odor gradients located throughout the home and contiguous areas raises questions as to the odor sources. To test the possibility that individually recognized conspecifics might be contributing factors in this scheme, an odor discrimination study was initiated in 1969.

Method

An olfactometer was designed and built that would (1) reduce the mixing of two convergent air streams at the point where discrimination would take place and (2) allow easy but thorough cleaning procedures following each individual test (fig. 6). All glass and plastic sections were made in multiple such that all could be soaked in soapy water for 24 hr prior to being used. Compressed breathing air was introduced into the system by way of a constant pressure regulator and then split into two air streams destined to be laden with different test odors within the sample bottles. The wind velocity in the main discrimination tube averaged about 0.2 m/sec. However, momentary velocity increases were occasionally used to stimu-

late movement. Prior to testing, the sample jars were moistened with 10 cc of water in order to raise the relative humidity of the air entering the discrimination tube.

Salamanders for testing were collected by searching woodland areas at night until two adult salamanders of the same sex were observed within 3 m of each other. These, classified as familiar with respect to each other, were captured singly and put into separate transport jars. A third conspecific also of the same sex was then captured at least 30 m away (well away from the home areas of the other two) and put into a third jar. This animal was considered to be unfamiliar relative to the first two. The three were then immediately taken to the laboratory where the olfactometer was set up in the dark.

The unfamiliar and one of the familiar salamanders were introduced separately into the sample jars which were arranged at random to the right or left side of the olfactometer. The second familiar salamander became the test subject. This animal was enclosed in the approach section of the discrimination tube between a 3-mm mesh screen partition and a screen-covered hollow plug. When slow investigatory movements were observed away from the partition in front of the divided section of the tube, the partition was lifted and the animal's eventual movement into either side of the tube was recorded. A red light was directed up the discrimination tube and observations were made through a pin hole in the black cloth that covered the entire apparatus.

Results and Discussion

The results of the 34 salamanders tested indicate that the animals initially preferred to enter the side of the tube corresponding to the side of the system that enclosed the familiar conspecific (fig. 6). Later in the season the preference was essentially reversed. Before July 9, 15 of 17 salamanders chose the familiar conspecific side; while after July 9, only six of 17 animals chose the familiar side. The difference between the two periods is significant ($p<.01$). No right or left bias (13L:21R) in the system was significant. Of interest to note is the observation that breeding activity increases gradually in July to a peak in the latter part of August (subjective impression from 4 years of observations in the field at night).

During June a different series of tests were also conducted. Salamanders collected in the field were given a choice of odors either from a 10-cm diameter humus sample collected 0.3 m from where the salamanders were captured (familiar sample) or from a sample collected from a similar habitat over 30 m away (unfamiliar sample). Of the 10 salamanders tested, no preference was observed for either the familiar or unfamiliar samples. However, the upward trend generally coincides with the decreasing trend in the cumulative frequency of familiar conspecific choices (fig. 7). Although quite preliminary, these results suggest the possibility that different olfactory cues may be used at different time of the season for identifying the home area.

In any event, the results suggest that the individual odors of conspecifics living in and around the home area of a given salamander may be quite important as site specific odor cues. If the animal were displaced, these odor cues could be used to relocate the home area. The same cues could also be used to adjust both local movements and, perhaps, movements favorable for spacing and reproductive relationships. The climbing behavior exhibited by this species on surface objects and tree trunks at night could easily be a functional part of such a chemical information system (ref. 2). In effect, then, the results of

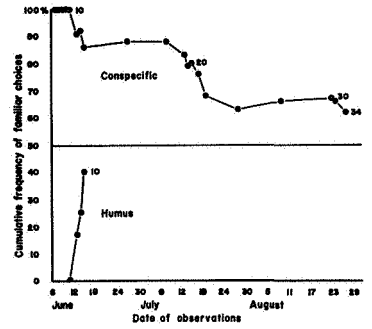

FIGURE 7. Cumulative frequency of familiar choices in the olfactometer apparatus as a function of time. Only the cumulative number of salamanders at intervals of 10 are indicated, with the exception of the last salamander tested. For example, 80 percent of the 20 salamanders tested (16 in number) by July 12 had preferred the familiar conspecific odor.

the olfactometer experiment support the explanation based on olfactory cues given for the results of the odor displacement study. Clearly, however, additional studies are needed before conclusive statements can be made.

HYPOTHESES

In review, the homing ability of *P. jordani* is highly oriented, direction-independent, and distance-dependent. The ability is manifest in salamanders that are displaced into areas that had not been occupied previously. Vision is not required for the response although a functioning olfactory system seems essential. In attempting to relate these characteristics to those of each of the three levels of homing orientation proposed by Griffin (ref. 13), and later clarified by Schmidt-Koenig (ref. 14), I found it difficult to classify the homing response of *P. jordani*. Piloting or type I homing was excluded because *P. jordani* displaced into previously unoccupied areas returned by home-oriented movements and not by random movements or search patterns. Directional orientation or type II homing was excluded because the homing response was direction independent. Finally bicoordinate or reverse displacement navigation did not seem directly implicated because *P. jordani* probably rely on familiar odor cues emanating from the home area for directional information. Although entirely appropriate for levels of bird orientation for which it was designed, the classification should receive additional emphases if it is to be more broadly applicable to other sensory systems and vertebrate groups.

The modification of the classification would seem to require the following adjustments relevant mainly to piloting. The phrase "familiar landmarks" should be changed to "direct sensory cues." The former words imply mainly visually perceived information, while the latter words include the use of other sensory cues that are specific to and occur in spatial association with the home area or goal. The concept of "familiar territory" should also be considered. The definition of what constitutes such an area is a function of the particular sensory associations considered. The familiar auditory or tactile components of a region may denote an area considerably different in size and meaning from one based on familiar visual or auditory stimuli. In the broadest sense, the area occupied at a given instant can be considered familiar as long as direct sensory cues are still perceivable. Thus *P. jordani* could use familiar olfactory cues to home from areas that had never been occupied previously, and in so doing be "piloting." Random movements or search patterns might be expected then when the salamander is displaced beyond the limits of this direct sensory information.

The third level of homing orientation should receive an additional emphasis in the nature of the coordinates. Instead of using

global coordinate systems, a fairly sedentary animal by similar processes could use local gradients to achieve what I would like to call "local gradient navigation." This type of navigation would require (1) the existence of two or more fairly linear but non-parallel gradients of physical or chemical variables, (2) a region including and extending beyond the home area of the animal through which the slope and direction characteristics of the gradients would be consistent, (3) an animal sensitive to different measures of the physical or chemical variables in question, (4) an animal with the knowledge of the direction of the local gradients, (5) an animal able to "remember" in some way the home values of these measures during displacement, and (6) an animal able to compare the home and release values, either concurrently or alternately, and to move in such a way that the home reference values would be restored.

The degree of displacement necessary before differences in the variable measures could be detected, of course, would be proportional to the slope of the gradients. The maximum effective distance of such a mechanism would be reached when, in other areas, different slope or direction characteristics of the same variables are encountered. In effect, then, the same general characteristics used to define long-range bicoordinate navigation, i.e., the use of bicoordinate information obtained from cues that are not in direct association with the home area of goal, also define the characteristics of this local mechanism. Subtle local gradients of the types just mentioned could have aided *P. jordani* in its homeward movements.

Another type III homing mechanism that *P. jordani* could have used, and one needing some reconsideration on a local scale, is inertial navigation. The potential cumulative error associated with linear and angular acceleration determinations would probably be less critical during shorter range displacements or homing movements, providing the frequency of these determinations was proportional to distance. In fact the mechanism could be expected to produce the direction-independent and distance-dependent results recorded. Perhaps relevant to the possibility of this mechanism operating in *P. jordani* is the occurrence in this species of a specialized substrate vibration detection system (ref. 15) which could act as an independent sensor of movements imposed upon the whole body. This system includes an opercularis muscle that connects the opercular cartilage of the middle ear to the suprascapular process of the shoulder blade. Also of potential importance to an inertial mechanism is the fact that *P. jordani* moves with the long axis of the body generally aligned in the direction of movement. This alignment would tend to facilitate detection of direction changes because of bending forces along the body axis. Animals moving through less fixed and more homogeneous media (air, water) would not likely have this advantage to the same degree.

In conclusion, the actual homing mechanism in *P. jordani* remains unknown. However, the results recorded to date can best be explained by a mechanism involving oriented movement into the wind when occasional familiar odors from the home area are detected and when environmental conditions are moist enough to allow prolonged surface exposure. That such a mechanism may be supplemented by inertial cues or by local physical or chemical gradients is a reasonable possibility.

ACKNOWLEDGMENT

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DISCUSSION

QUESTION: Have you any examples of disorientation on longer distances?

MADISON: In a previous study (*Animal Behaviour,* 19(1), 1969), I reported on a series of displacements of 6 to 300 m with the same species. Successful homing seemed to be a function of displacement distance.

EMLEN: Have you done any experiments with displacements in different directions?

MADISON: Yes, in the same study animals were displaced in four directions parallel and perpendicular to a mountain slope. There was no difference between any of the displacement groups. In other studies salamanders homed successfully following displacement in both directions across mountain ridges and streams.

JACOBS: Have you tried displacing them vertically, up in a tree?

MADISON: No. However, I have recorded the frequency of climbing by displaced and control salamanders (Madison and Shoop, 1970). There is a significant correlation between animal displacement and their frequency of occurrence in trees soon after release. This behavior could facilitate the detection of home associated odors.

WILLIAMS: Did you try any work with vibrations? These animals live near a stream which produce characteristic vibrations at various points.

MADISON: Vibration could give one coordinate of a bicoordinate system in terms of a vibration intensity gradiant. However, another physical or chemical gradiant along a different axis would have to be used before local navigation could be possible.

WILLIAMS: Animals pay attention to more than one cue. It is common that they use a landmark system.

MADISON: *P. jordani* is probably quite sensitive to the physical and chemical environment in which it lives. Removed almost totally from its normal environment, the salamander may very well have but just one sort of direct familiar information about the home area and just one sensory system able to receive the information. I prefer not to regard occasional familiar odors, which are detected in areas removed from the home area, as landmarks. The definition of what constitutes a landmark is quite difficult when considered in terms of the various kinds of sensory input that are possible.

EMLEN: About redundancy of systems: If a blinded animal comes home, that doesn't say that it can't use visual cues. That says that it has enough information available without visual cues. In another situation it may rely heavily upon visual information. Experimental results can be, and have been, misinterpreted by ignoring the redundant nature of orientation systems. That is an important point.

MADISON: That is a good point. One would think, however, that the anosmic animals might home using their visual system—if intersystem redundancy in this species works both ways.

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SESSION V

Sensory Mechanisms—Other Senses

Chairman, MARTIN LINDAUER

Anemomenotactic Orientation in Beetles and Scorpions[1]

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SCORPIONS, living in North African semideserts are—in spite of disrupting experimental interferences—able to maintain a certain direction in their natural environment in the dark on a plane surface. Under comparable laboratory conditions, excluding the possibility of light or gravity orientation, they can orient themselves if a directed air current passes over the "arena."

In most cases the scorpions do not run necessarily with or against the wind, but rather maintain constant angles to the air current for anywhere from minutes to many hours. They are running anemomenotactically (ref. 1). Under identical conditions many species of beetles also orient themselves to air currents (refs. 2 to 4). The main problems to be solved in the study of anemomenotactic orientation are:

(1) Which physical qualities of the air current have an influence on the anemomenotaxis?

(2) With which sense organs do beetles and scorpions perceive wind directions?

(3) Which physiological mechanism is the basis of anemomenotactic orientation?

(4) What is the biological significance of anemomenotaxis in beetles and scorpions?

With respect to these problems, more study has been done on beetles than on scorpions. Therefore, due to lack of space, I shall discuss mainly some of the results obtained in experiments with dung beetles (*Geotrupes silvaticus, G. stercorarius, G. armifrons, G. niger, Scarabaeus variolosus*) and tenebrionid beetles (*Tenebrio molitor, Pimelia grossa, P. tenuicornis, Scaurus dubius*).

METHODS[2]

The horizontal arena (diameter 1 m) was placed in an octagon that screened out daylight and ambient air currents. The directed horizontal wind is produced by adjustable ventilators (with a rotating drum fan). After every run to the brink of the arena the beetles are returned to the center of the running area. The direction of the wind stream in each experiment was repeatedly changed.

At first only pure anemomenotaxis was to be investigated, and every possibility of incident-light orientation had to be excluded.

[1] These investigations were supported by the Deutsche Forschungsgemeinschaft.

[2] For more details see Linsenmair (refs. 3 and 4).

The beetles, reacting to red light with a wave length of over 6100 A (Osram 5463), were blinded by an opaque laquer. In dung beetles it was sufficient to cover the upper half of the divided eyes in order to exclude directing effects of the red light. Experiments with scorpions, with all eyes laquered, had always to be performed under red light because only then light reactions not mediated by the eyes could be avoided.

RESULTS

Physical Qualities of the Air Stream

The lowest wind velocity which would evoke menotactic orientation in dung beetles was about 0.15 m/sec; it was about 0.4 m/sec in *Pimelia* and about 0.5 m/sec in *Tenebrio*. The limiting velocities against which the beetle can not move are 2.5 to 4.5 m/sec, depending on size of the beetle and the nature of the surface on which it is running; this upper limit also applies to scorpions. In the lower range however scorpions react anemomenotactically to air currents with speeds of only 0.02 to 0.05 m/sec. For scorpions and beetles, changing of wind velocities—within the mentioned limits—has no effect on the anemomenotactic angle (refs. 1 and 3).

Beetles can orient themselves in discontinuous horizontal winds, if the wind puffs are not too short and the intervals of still air are not too long. Experiments with dung beetles and scorpions on an extremely rough surface that caused strong air turbulences show that orientation is not greatly affected by such disturbances (ref. 3).

Wind Perception

Weeks after an amputation of both antennae a beetle does not orient to air currents. However, it was found that as few as two segments of the flagellum on each antenna are sufficient to allow a dung beetle to orient anemomenotactically if the wind velocity is at least 1 m/sec. Fixing joints of the antenna by laquer shows that only the flexibility of the pedicellus-flagellum joint is necessary for anemomenotaxis. Movements in this joint—as we know from many insects—are perceived mainly by the Johnston-organ (refs. 5 to 8). It therefore seems obvious that also in the running beetle the Johnston-organ perceives air currents and detects their direction. In scorpions the trichobothria fulfill these tasks.

Physiological Mechanism

There are two theories to explain the special performances of menotaxis:

(1) Janders (refs. 9 and 10) "compensation theory"

(2) Mittelstaedts (refs. 11 and 12) theory of the "reciprocal modulation of bicomponents"

Because Janders' theory is less complicated, we shall see first whether or not this theory can explain the experimental findings.

The functional organization of menotaxis is explained by the compensation theory in the following way. The bases for menotaxis are the two basic orientations, the positive and the negative taxis. For example, in the positive basic orientation a deviation from the positive basic direction (i.e., a deviation from the position exactly against the stimulus direction) causes a reactive turning excitation. This "afferent turning tendency" leads, over the smaller angle, back to the positive basic direction and is in strength dependent on the amount of deviation. In switching over from the positive to the negative basic orientation the turning directions of this turning tendency are reversed, thus inducing the animal to turn to the negative basic

direction via the shortest path. Basic orientations are assumed to participate in menotaxis, determining patterns of turning tendency directions and turning tendency strengths as in basic orientations. All menotactic runs not deviating more than 90° from the positive stimulus direction are supposed to be based on positive basic orientation (the turning tendency therefore always leading to the positive basic direction), whereas those aiming in the opposite directions (± 90° to 180°) are supposed to be based on negative basic orientation. Because the turning tendency always would force the animal to turn back to the basic direction of the "switched on" basic orientation, the compensation theory postulates the existence of a second, opposite directed and centrally generated, turning excitation—the "efferent course order." If the menotactic set angle is reached, the two equally sized turning excitations, opposite in their directions, are assumed to neutralize each other.

One should be able to disturb this equilibrium by, for example, suspending the turning tendency (by the sudden removal of the directing stimulus). In figure 1, results of such experiments are summarized. In the anterior half of the circle (quadrants I and IV) the beetles—in a highly significant percentage—turn away from the direction of the wind stream; in the posterior half (quadrants II, III) however they choose the opposite turning direction, with respect to the wind direction. The angle size within a quadrant does not influence the direction of the turning. These results are in accord with the compensation theory; not only the course order becomes apparent as a directed turning excitation, but the demonstration of opposite turnings in adjacent quadrants makes the participation of both basic orientations in anemomenotaxis very probable. In the anterior half of the circle the beetles turn away from the

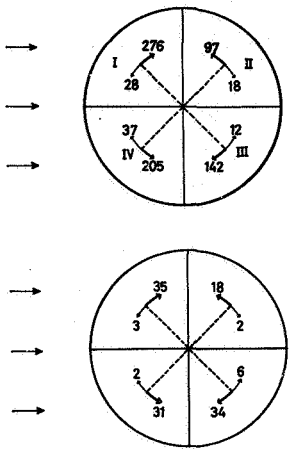

FIGURE 1. Directions of turning movements induced in anemomenotactically oriented *Geotrupes* (1a) and *Pimelia* (1b) by a sudden interruption (see Linsenmair ref. 3) of the air current. Arrows pointing toward the circle in all graphs symbolize wind direction.

positive basic direction, while in the posterior half they turn away from the negative basic direction. This distribution of turning directions, after a suspending of the turning tendency, has to be expected if the basic orientations are, as postulated by the compensation theory, responsible for the directions of the turning tendency, and if, with respect to the corresponding set angle, the turning tendency always is compensated by an opposite-directed course order.

In figure 2, the distribution of the running directions of four dung beetles is presented. Their individual preference direction lay between 27° and 32° right of the positive basic direction. The runs not aiming in the preference direction are not evenly distributed over the rest of the circle, but are concentrated in an adjacent quadrant. If one compares the mean angle deviation of the runs from the next basic direction in the two quadrants most often chosen, then the following null hypothesis proves correct: With re-

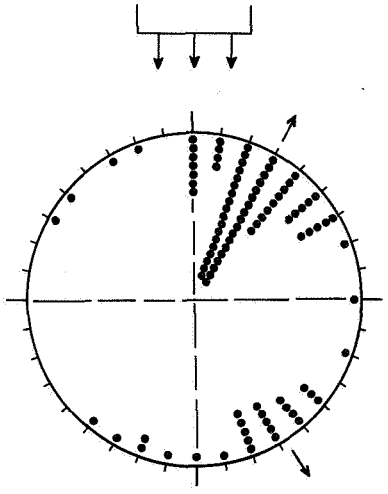

FIGURE 2. Distribution of the anemomenotactic courses of four dung beetles, all of which maintained a preference direction of about 30° to the right of the positive basic direction. The two arrows pointing away from the circle show the preferred angle sizes within the two quadrants most often choosen. Every point represents two runs.

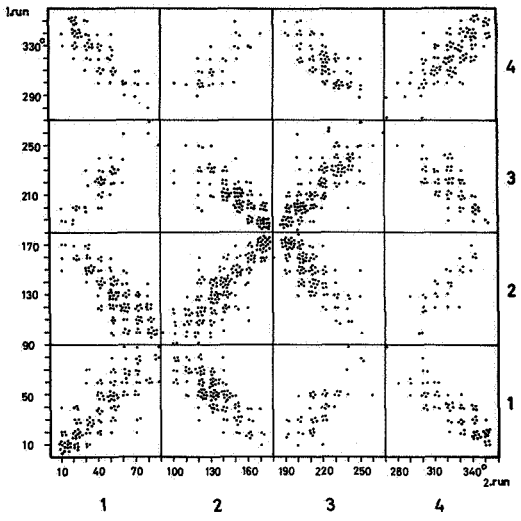

FIGURE 3. Correlation diagram: Evidence of the fourfold intramodal angle size transposition in *Geotrupes*. All correlation modi are highly significant ($p < 0.005$).

spect to the basic directions all four dung beetles in both quadrants kept the same preference-angle size with the same standard deviation. While the choice of the quadrant may be strongly influenced, the mean deviation from the basic directions in the intact beetle normally remains constant under different conditions as well (see ref. 3). When one correlates two succeeding runs of dung or tenebrionid beetles in different quadrants, one gets the results shown in figure 3. A correlation analysis proves that a beetle running successively in two of the four quadrants generally maintains his angle size. This "intramodal transposition" (ref. 13) is easily understood in assuming that:

(1) Course orders cannot lead to deviations from a basic direction exceeding 90°

(2) That the turning direction of the course order and/or the turning direction of the turning tendency may be reversed, without changing the strength of the course order (ref. 3)

These findings are also not contradictory to the compensation theory.

By another method, information about the physiological mechanism of anemomenotaxis has been gained which confirms the mentioned findings.

Under natural conditions air currents normally effect both antennae. Here the question arises about the kind of interaction between the specific sense organs of the pair of antennae. Figure 4 shows a typical result. After amputation of one antenna (or after blocking the pedicellus-flagellum joint by laquer) the mean size of the running angle increases. In the case that the size of the course order is not affected by the exclusion of one antenna, the elimination causes a decrease in the strength of the turning tendency. This supports the hypothesis of a synergistic interaction of the paired antennal

organs and opposes the main alternative hypothesis of an antagonistic—i.e., tropotactic—interaction. The fact that it is of no influence on the menotactic angle size whether the left or the right antenna is amputated supports also the idea that the excitations of the paired sense organs are summed up.

Figure 4 shows that the elimination of one antenna leads to an approximate doubling of the angle size. This result suggests that the antennae are equivalent synergists. If this assertion is valid without limitations, then there should be a range of running angles, in which the halved turning tendency of the amputated beetle cannot compensate the unchanged course order. In these cases the beetle should rotate. This expectation is proved only partly by results presented in figure 5. Indeed some beetles rotate which had, when intact, kept angles of about 30° or more. But in this range of angle sizes, after an elimination of one antenna, one finds not only very different augmentations of the running angle, starting from the same "intact-angle," but also significant reduction of angle sizes.

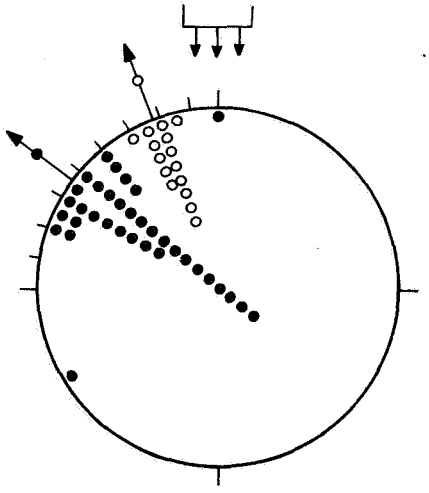

FIGURE 4. Distribution of the running courses of a dung beetle before (circles) and after (points) complete amputation of its right antenna.

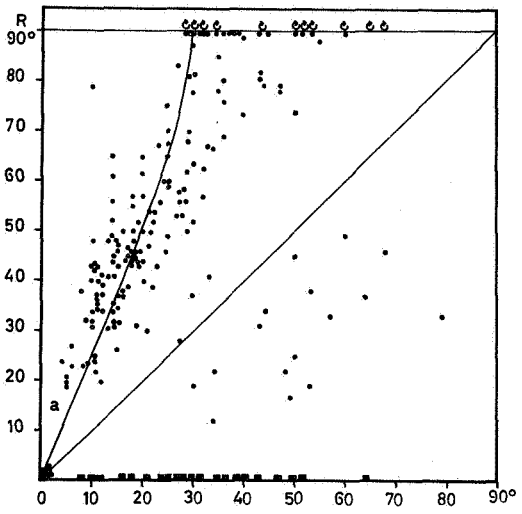

FIGURE 5. Mean angle sizes of the run series of dung beetles (n = 139 beetles, about 11 000 single runs) with one antenna excluded (ordinate) independent of the angle size maintained before the exclusion (abscissa). Bent arrows within the R-line symbolize rotations of the beetles. Some beetles, after an exclusion of one antenna, change over from the anemomenotactic to a basic (anemotactic) orientation (squares on the 0° line; see Linsenmair ref. 4). The curve *a* is to be expected if there is a sine function between the stimulus direction and the strength of the turning tendency, and if the exclusion of one antenna is always followed by a 50 percent reduction of the turning tendency strength. Because of the four-fold intramodal transposition, and other experimental evidence, it is justified to treat the size of a menotactic angle (measured as the amount of angle deviation from the next basic direction) without taking into account its direction (within the range of 360°).

Beetles running first with intact antennae, then with one antenna eliminated by reversible laquering, and finally again with both antennae intact show the reactions presented in figure 6. If the running angles maintained in the "preliminary experiment" are not big-

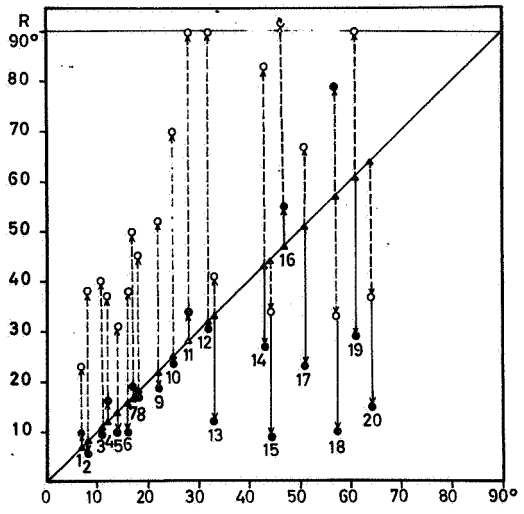

FIGURE 6. Changes in the mean angle sizes after a reversible exclusion of one antenna (ordinate). Triangles are mean angle sizes in the "preliminary experiment" (abscissa). Dashed arrows with circles are directions and amount of changes in angular size in the "main experiment". Solid arrows with points are changes of angular size in the "control experiment" in comparison with the angle size in the preliminary experiment. (Dashed dotted arrow in beetle 18: sudden spontaneous change of angular size, from about 10° to about 80°, in the control experiment.)

ger than about 30° then the angle sizes are augmented significantly in the second experiment, the "main experiment." In the third experiment, the "control experiment," the again intact beetles resume the same or nearly the same angles as in the preliminary experiment. The augmentation of the running angle sizes in the main experiment therefore has to be attributed only to a reduction of the strength of the afferent turning tendency.

Angles bigger than 30° in the preliminary experiment may be augmented or diminished. The amount and the mode (i.e., increase or decrease) of the change in angle size cannot be predicted. What can be predicted, however, in these beetles is amount and mode of change in angular size from the main to the control experiment: The angular size always is approximately halved (see fig. 6). The menotactic angles then maintained by these beetles in the control experiment are regularly smaller than in the preliminary experiment. This fact obviously demonstrates that the strengths of course orders, leading to running angles in excess of 30° in the preliminary experiment, are in all beetles diminished, which can still keep a straight course in the main experiment.

Preference angles of about 90°, after elimination of one antenna, are based on course order strengths leading in the intact beetle (in the control experiment) to angular sizes of about 30°. Angles larger than 30° cause rotations in the main experiment (see fig. 6, beetle No. 16) if the course order strength is not reduced. These findings together with the varying scale of angle enlargements in the range from 0° to 30° (see fig. 5) make a sinusoidal relationship between stimulus direction and strength of turning tendency very probable.

Elimination of one antenna is not followed by a loss of the essential qualitative performances of the anemomenotaxis. Beetles with only one intact antenna can determine the wind direction. They can steer anemomenotactically anambiguous directions relative to the air current and are—after a forced deviation—able to turn back to their preferred direction over the smaller angle. Quantitatively—in evaluating the stimulus direction by a certain strength of the turning tendency—one antenna shows only half the capacity. As would be expected, if there is an equilibrium between two antagonistic forces, the course order has a doubled efficiency after the turning tendency is halved. The running angle is doubled (see previous discussion of

intact angles larger than 30°). Likewise, the course order efficiency is always halved if, after a reversible elimination of one antenna, the beetle runs again with both antennae intact. Especially important is the evidence that the menotactic angle size, after enlargement caused by an elimination of one antenna, never exceeds 90°, as measured from that basic direction to which the turning tendency leads and from which the course order deviates. If a course order leading to a running angle larger than 30° is not diminished after elimination of one antenna, the beetle does not run into the adjacent quadrant, but rotates. In a beetle running into an adjacent quadrant after one of its antennae was eliminated, it can always be demonstrated that it transposes angles (ref. 4).

Mittelstaedt (refs. 11 and 12) makes two objections, one depending on the other, against the compensation theory:

(1) The theory offers no explanation of how an animal can steer a menotactic course beyond 90°.

(2) The theory does not explain the equally sized and equally directed shift of the stability and the lability positions.

A purely additive superposition of a course order, with the sign remaining constant, over the sinoidal turning tendency must lead to an approximation of the positions in which both opposite turning excitaing excitations are in a labile equilibrium—position—and the position in which the turntions are in a constant equilibrium—stability They coincide with each other at ± 90°. lability position (refs. 11 and 12, 14 and 15). Therefore courses deviating by 90° from a basic direction should be very unstable, and angles beyond 90° could not be steered by such a mechanism. Numerous experimental results show, that in the anemomenotaxis of the investigated beetles a course order of the maximum amount can not deflect the beetle to a deviation exceeding 90° from a basic direction. But still there would be the instability of 90° courses, if the course order was superimposed by addition (demonstrated by Schöne (ref. 14) in the photomenotaxis of dydiscid larvae). Above all, beetles not always were able to turn back to their preference direction over the smaller angle. Deviations from this principle of "the shortest turning way" are not found in a group of beetles orienting anemomenotactically. Also some beetles, when one antenna is eliminated, turn promptly, and some turn much later over the smaller angle back to their preference direction. Stability and lability positions thus lie opposite to each other in anemotaxis as well as in anemomenotaxis. How does this finding fit in a compensation mechanism?

The turning tendencies in the right and the left half of the circle have different signs, if the beetle runs in a basic direction; in deviating into one half it turns to the right, in the other half, to the left. The opposite signs do not disturb the anemomenotactic orientation mechanism, because a beetle cannot run at the same time in both halves of the circle. In supposing that also the signs of the course order are always reverse in the anterior and posterior half of the circle, all previous results concerning the anemomenotaxis of beetles are consistent with a compensation mechanism (figs. 7 and 8; compare to ref. 16).

Biological Significance of Anemomenotaxis

Whenever possible scorpions orient relative to landmarks. Sometimes light sources (e.g., the Sun or Moon) give the essential directing stimuli. As soon as one eliminates visual orientation possibilities, it turns out that scorpions permanently take notice of the direction of the wind. Where vision served before, the scorpions learn to keep their

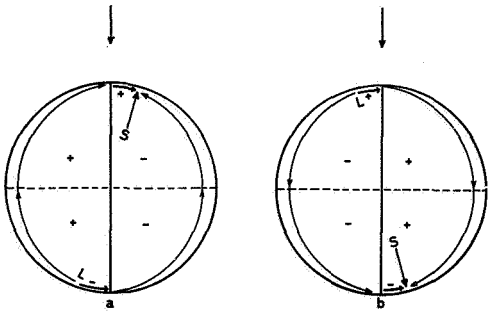

FIGURE 7. Turning movements (directions of arrows) observed after deviations from the stability position S in anemomenotactic oriented beetles. In L—the liability position—turns to the right and to the left are equally frequent, in all other cases the beetles take the shorter way. Thick arrows show the ranges in which observed turning movements are opposite to those of a positive (7a) or negative (7b) anemotactic beetle. It is proposed that these turns are induced by the course order, which is assumed to act in the anterior and posterior half of the circle with reversed signs of the turning direction. Between 7a and 7b an angle transposition took place, in which not only the taxis was switched over (the signs of the direction of the turning tendency are reversed in the right and the left half of the circle) but also the sign of the course order direction. (Movements to the right are "+", to the left "—".)

course by pure anemomenotaxis (or anemotaxis). As far as is known scorpions possess no sense of smell. Probably the main task of anemomenotaxis is to provide a sense of space orientation which, like in many cases photo- or geomenotaxis, allows the animal to keep a straight course. Because the scorpions are nocturnal, and because in their natural environment there is a nearly continuous wind varying only occasionally in direction, the anemomenotaxis is of great value.

In the lives of the investigated beetles, stimuli perceived by osmoreceptors are of great importance. While at very short range a pure osmotropotactic or osmoclinotactic orientation may lead to the source of a smell (refs. 17, 18 and 19), one can hardly imagine how such a mechanism could work in an osmic orientation over long distances. Several authors (refs. 20 to 23) suggest that long distance olfactory orientation is not possible without positive anemotaxis.

Also those animals in which an osmic sign stimulus releases a positive anemotaxis are forced to search the sign stimulus. Here one should look for the main task of the beetles anemomenotaxis. This supposition is supported by observations of different species of dung beetles in their natural habitat; in search for food, running dung beetles choose a menotactic course to the wind direction. Thus they can "oversmell" a maximum area in a minimum of time.

If the beetle's attention is drawn to the smell of dung while flying he often lands more or less far from the dung; as this beetle, also a scarabaeus—having lost his dung ball on a slope—knows in which approximate area it has to search. In such cases one does not only recognize the biological significance of anemomenotaxis but also that of the ability to transpose anemomenotactic angle sizes intramodally. The beetles, maintaining at first an angle of say 30° to the right of the positive basic direction, after a run of some length make a turn of 60°, maintaining then a course of 30° to the left from the positive basic direction. The result is a zigzag course, which is especially appropriate in tracking a smell source of which the approximate position is known.

Thus the anemomenotaxis is a very important part in the appetitive behavior of dung beetles "waiting" for an olfactory sign stimulus. As soon as the dung beetle has found that sign stimulus it changes its direction and runs against the wind. The question how this positive anemotaxis and the osmic orientation interact has to be answered by further experimental investigations.

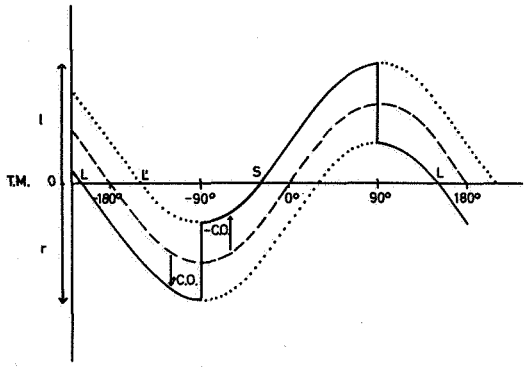

FIGURE 8. In a pure additive superposition of course order (C.O.) over sinoidal anemotactic turning tendency (dashed sine curve, set angle 0°) stability and liability positions are, in increasing angle sizes, approaching each other; for example, S and L′ in the upper, partly dotted, partly solid, sine curve. They coincide in ± 90°. [A course order showing a turning direction to the right is called positive (+ C.O.), a course order with a turning direction to the left negative (— C.O.).] In the case of the upper and lower sine curve, an animal, deviating into the range from —150° over 180° to +150°, could not turn back to its set direction (—30°) over the smaller angle [r equals turning movements (T.M.) to the right, l equals turning movements to the left]. In assuming reversed signs of the course order in the anterior and posterior half of the circle, one attains the solid curve: Stability position S and lability position L now lie opposite to each other. In deviating from its set course, the animal always can turn back over the shorter way.

SUMMARY

1. Scorpions and beetles can orient menotactically to the direction of horizontal air currents. Changing the wind velocity, within the range releasing anemomenotactic orientation, does not influence the size of the menotactic angle. The anemomenotactic orientation is not seriously affected by discontinuities and turbulences of the air current.

2. In scorpions the trichobothria perceive the direction of the wind. In the investigated beetles air current directions are perceived by sense organs excited by movements in the pedicellus-flagellum joint.

3. The experimental findings suggest a compensation mechanism as the basis for anemomenotactic orientation in beetles. A straight menotactic course can then be maintained when the "afferent turning tendency" is compensated by an opposite directed "efferent course order" of equal size. Both basic orientations, positive and negative anemotaxis, participate in the anemomenotaxis and determine the pattern of turning directions and turning strengths of the turning tendency. The function between the strength of the turning tendency and the stimulus direction is sinoidal. As to be expected in a compensation mechanism the maximum size of a menotactic angle is 90°. By maintaining the strength of a course order and by reversing their turning direction and/or the turning direction of the turning tendency the beetles can transpose menotactic angle sizes. Also the fact, that in anemomenotaxis the stability and the lability position lie opposite each other is consistent with a compensation mechanism; we only have to assume that the turning direction of the turning tendency in the right and the left half of the circle, and the turning direction of the course order in the anterior and posterior half of the circle are always reverse.

4. The interaction of the paired antennal sense organs of the beetles perceiving wind directions is synergistic. The exclusion of one antenna is followed by a 50% reduction of the strength of the turning tendency.

5. The main biological significance of anemomenotaxis in scorpions is suggested in space orientation. Whereas in beetles it is evident, that the anemomenotaxis is an important part of the appetitive behavior of beetles "searching" for olfactory sign stimuli.

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Azimuth Orientation of the Dragonfly (*Sympetrum*)

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RELATIVELY LITTLE IS KNOWN about the migratory behavior of the dragonflies. Sole summer populations of *Anax junius* in Canada are thought to be maintained by migration from the southern range of their distribution (refs. 1 and 2). Other species, such as *Sympetrum rubicundulum* (ref. 3) in North America, and *Sympetrum striolatum* (ref. 4) and *Aeshna mixta* (ref. 5) in Europe, have been recorded as flying south in early autumn. If these northward and southward movements of the dragonflies are, as they appear to be, unidirectional and well oriented, then it becomes of interest to find out the factor or factors determining the orientation mechanism in migration.

In the past only a few remarks have been made on the orientation of the settling dragonflies. Adults of *Sympetrum sanguineum* are reported to settle in large numbers on telegraph wires or fences. The orientation of these settling individuals is said to be very constant, being related to the direction of incident illumination, so that they face away from the darkest part of their immediate surroundings (ref. 6). This habit of settling en masse on telegraph wires and adopting a constant orientation is also shown by other species of the dragonfly (*Sympetrum costiferum,* Kennedy, ref. 7, *Cratilla calverti,* ref. 8). However, the factor or factors determining orientation are yet to be convincingly demonstrated.

While collecting the dragonfly *Sympetrum* species in the field as an experimental material, we noted a peculiar tendency of the alighting individuals to take a particular direction relative to the Sun. This phenomenon attracted our attention because of possible connection to the migratory behavior as well as to the dorsal light reaction of the species that we have already partly described (ref. 9). Cursory field observation revealed that the direction of orientation is different at different times of the day as it appeared to be somehow related to the displacement of the azimuth of the Sun.

Directional phototactic orientation of many kinds of animals, both in the field and in the laboratory, has been amply described (refs. 10 to 12). There are, however, a small number of observations on the orientation of alighting insects. The contribution of the dorsal light reaction to the equilibrium reaction of the dragonfly *Anax imperator* has been analyzed in detail by Mittelstaedt (ref. 13),

mainly in free flying animals. Some other observations exist, but they place emphasis on the reaction of various insects either around their longitudinal axis (banking response) or transverse axis (pitching response) when the light source is placed around those axes (refs. 14 to 16).

Only one report exists on the azimuth orientation of the dragonfly in the horizontal plane. Thus Jander (ref. 17) demonstrated the response of *Calopteryx splendens*, illuminated from various directions in the horizontal plane; but again the emphasis was on the change of posture, not on the change of direction.

In this paper, evidence is presented of directional orientation of the alighting dragonfly relative to the azimuth of the Sun, and an indication is given of the contribution of the wind direction to this orientation. Some preliminary experiments to seek out a possible operative receptor for this orientation will also be noted.

Observed individuals belong to genus *Sympetrum* (Libellulidae, Odonata), of which more than 95 percent are *Sympetrum frequens* Selys, with a very few being *S. darwinianum* S. and *S. infuscatum* S. However, no particular difference in behavior was noticed among those species.

FIELD OBSERVATION

General Behavior

Field observations were performed in an open field on the university campus, which measures about 30 m in east-west direction and about 100 m in north-south direction, and is surrounded with low bushes and bordered with some trees about 5 m high at the north-east corner, the nearest of which stands about 30 m apart from the field's edge.

To avoid possible interference by reflected sunlight from the nearby substratum, data were collected from the dragonflies alighting exclusively on tops of bamboo sticks projecting about 2 m above the ground. It is of interest that there were no directional deviations of the individuals when the tops were lower than 2 m. However, there were directional deviations when the dragonflies were on flat surfaces of high reflectance, such as a white-painted signpost.

Around the end of September and early October, the daily active phase of the dragonfly appears to start at about 8:00 a.m. and continues almost to sunset, the general level of activity being greatly affected by the atmospheric temperature and the amount of sunshine. During warm, but not too hot, brighter, and less windy weather the number of individuals appearing in the field and alighting is more abundant. On the other hand, with winds of more than 2 to 3 m/sec, there is a reduction in number of individuals that can be observed. Thus the measurements were performed mainly on relatively calm days.

Azimuth bearing of the individuals alighting and the azimuth of the Sun were both measured with the aid of a compass attached to a clinometer for geological survey. Wind velocity and direction were measured with the aid of a thermistor-type anemometer.

Alighting individuals were approached from the rear, and the azimuth readings of their longitudinal body axes were measured through the sight attached to the clinometer. In each run of the measurement, 20 to 35 individuals could be observed alighting on the tops of bamboo sticks that were separated from each other by at least 2 m. The readings were taken as fast as possible, mostly within less than 10 min, and at the same time, the direction of the wind and also the wind speed were recorded together with the azimuth of the Sun and air temperature.

Dragonfly alighting appears to be performed in at least four distinct phases. First the dragonfly will approach the stick from a direction that is usually slightly deviated from the final orientation it will take after settling. Second, after a short hovering over the stick, it will alight. Third, while the wings are still stretched horizontally, it will make a final adjustment of the orientation by stepping around on the tip of the stick. During this phase, the head is still pivotted around. Finally, after a short while, the wings will be slightly drooped with the head held fast until startled by a moving object. It is rather curious to observe that when the dragonfly is startled, the first sign of alerting will appear as a jerking movement of the head and also a slight depression of the wings. If the dragonfly is startled with a stronger stimulus, it will take off but will often return repeatedly to the same spot through the almost identical course and alight again after a short while.

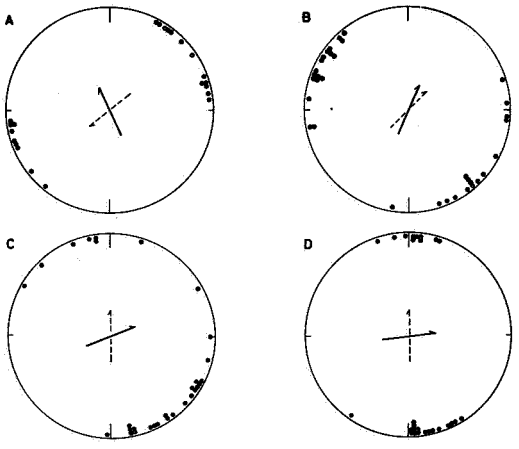

FIGURE 1. Changes in orientation direction of alighting dragonflies relative to the Sun's azimuth observed on one day. Azimuth is shown in heavy arrows and wind direction in dotted arrows. North is upward. (A) Time of observation: 9:40–9:50 a.m. Overcast: cloudless. Azimuth: SE 25–23° (measured from due south). Wind: NE, 0.2 m/sec max. Air temperature at 2 m above ground: 23° C. (B) 12:08–12:20 p.m. Cloudless. Sun: SW 22–26°. Wind: SW, 0.2–0.6 m/sec. 27° C. (C) 2:30–2:50 p.m. Cloudless. Sun: SW 65–71°. Wind: S, 1 m/sec max. 25° C. (D) 4:18–4:20 p.m. Cloudless. Sun: SW 82–85°. Wind: S, 1.5 m/sec max. 24° C.

At noon of a hot day (27° C), one individual was found to be taking a very peculiar posture while alighting on the ground: Its abdomen pointed upward almost in the direction of the rays of the Sun (close to 45 deg). In this manner it presented the minimum surface to the direct rays of the Sun, while the wings were drooping to cover the thorax. This kind of posture has been observed in tropical species (refs. 18 and 19).

Also around sunset, on a calm and rather cool day (15° C), many individuals were found to be perched headup on the vertical surfaces of nearby walls to expose their dorsal surfaces to the direction of the Sun. Otherwise, all individuals observed under the direct sunshine in the field have been observed to take a horizontal alighting posture, and their orientation was undoubtedly within a certain azimuth angle.

Orientation to the Sun's Azimuth

Four runs of the observation were performed in one day within their active phase to see the orientation change relative to the movement of the Sun. The measurements were performed on October 1, 1966, a quite calm and warm day. The air temperature around the measured dragonflies stayed 23 to 27° C; there was no overcast nor haze during the daytime. The first measurement (fig. 1A) was performed at 9:40 to 9:50 a.m., with the Sun's azimuth reading at 25 to 23°SE. The measurements were done on 22 individuals, all of which alighted on the tips of the bamboo sticks. The wind velocity was around 0.2

m/sec and from the northeast. Two groupings of dragonflies, both facing almost at right angles to the azimuth of the Sun were clearly recognized. In reference to the wind direction, 13 insects were facing windward, and the remaining 9 faced leeward. About 1½ hr later (from 12:08 to 12:20) 33 more insects were observed. They were also found to be distributed on both sides of the azimuth of the Sun (fig. 1B), the Sun having moved to 22 to 26°SW at this time of measurement and the wind blowing from SW at 0.2 to 0.6 m/sec. Although the wind direction was close to being parallel to the direction of the Sun, the windward individuals numbered 18 and the leeward ones 15. The distribution of the orientation appeared to be somehow more scattered than the previous observation in the morning hour. A possible explanation is the elevation of the Sun from the horizon which, at this time of day, was close to the maximum (45 deg). Two hours later 30 individuals were seen resting on the stick facing again in either direction. The windward portion of the oriented individuals was larger (24 to 6) with the wind blowing from the south at a velocity of 1 m/sec (fig. 1C). The final measurement of the series was done from 4:18 to 4:20, close to sunset. The clustering of the orientation angles of the individuals was at this time more significant than during the other two midday observations, and it was comparable to the results of first observation in the morning. Among the 27 insects, 17 were facing windward and remaining 10 leeward. It is now apparent that the orientations of alighting dragonflies is at least *primarily* related to the azimuth of the Sun throughout their active phase.

The same procedures were repeated on other days, and the results are represented in figure 2. The orientation phenomenon is seen to be the same as that described above. Figure 2A represents an observation performed

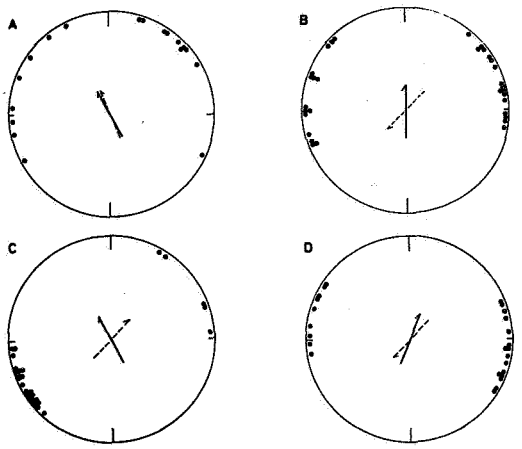

FIGURE 2. Direction of orientation of alighting dragonflies on separate days. (A) 9:20 a.m. Cloudy (80% overcast). Sun: SE 28°. Wind: SSE, 2 m/sec max. 16° C. (B) 11:30 a.m. Hazy but sunshine. Sun: S 0°. Wind: NE, 1 m/sec max. 18° C. (C) 9:35 a.m. Cloudless. Sun: SE 30°. Wind: SW, 0.5 m/sec max. 22° C. (D) 12:00. Cloudless. Sun: SW 20°. Wind: NE, 0.3-0.6 m/sec. 24° C.

on a hazy day (80 percent of overcast with thin uniform cloud and with the sun covered). There appeared to be more scatter of the orientation in this kind of weather. One difficulty in attempting to repeat the above observations on hazy days is that, when the overcast is even a little heavier, the number of dragonflies which settle is heavily reduced; therefore, one may not obtain a reliable number of observable individuals.

Since there is an apparent correlation of the azimuth of the Sun to the orientation of dragonfly, all the data are pooled and aligned with regard to the azimuth of the Sun (fig. 3). A notable characteristic of the orientation appears to be that the angle of the orientation relative to the Sun on both sides is slightly greater than a right angle. As seen in figure 4, a statistical analysis shows that the mean value of the angle of orientation with respect to the azimuth of the Sun is 98 deg

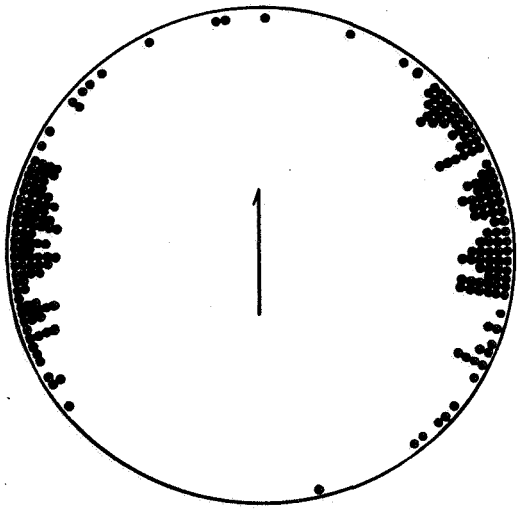

FIGURE 3. Dependence of orientation on the Sun's azimuth. All data are summarized by superimposing them relative to the azimuth. Arrow indicates azimuth.

on either side of the direction of the Sun's rays. A correlation coefficient of the oriented individuals facing the right-hand side of the Sun (that is, with one's back toward the Sun) is found to be 0.96, while facing the left-hand side the correlation coefficient is 0.94.

Effect of Wind Direction on Distribution

Although the orientation appears to be primarily determined by the azimuth of the Sun, the wind direction also seems to have some influence on the number of individuals in either half of the Sun's rays. Excluding the one observation in which the wind direction matched the azimuth, the number of individuals oriented in the windward half is without exception more than in leeward half. In total, the ratio was such that there were 2.6 times more individuals facing to the windward half. However, it should be clearly understood that the direction of the wind is not directly related to the dragonflies' orientations (fig. 5). The correlation coefficient between the wind direction and the direction of orientation of the animal is 0.23. This is low enough to exclude the direct connection be-

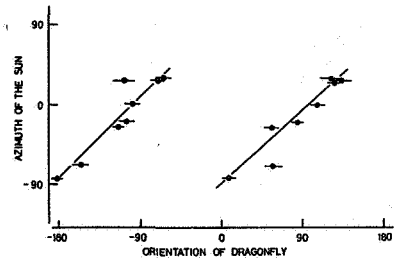

FIGURE 4. Dependence of distribution on wind direction. Data are shown relative to wind direction. Arrow designates direction.

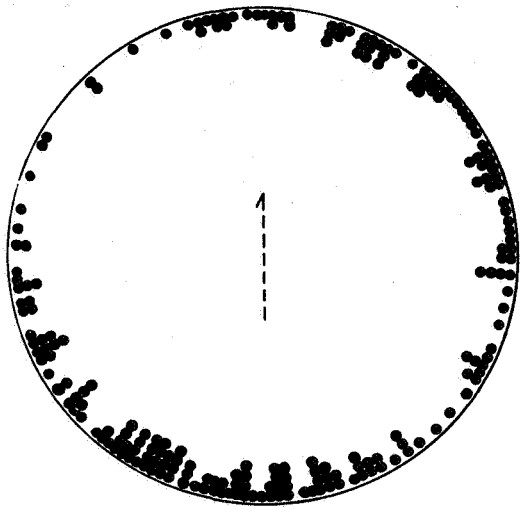

FIGURE 5. Orientation of dragonflies relative to the Sun's azimuth. Mean value of orientation directions for a number of observations is plotted with standard error against the azimuth. 0 indicates south in both ordinates and abscissae; positive number means easterly side and negative westerly. Regression lines are drawn by the least square method.

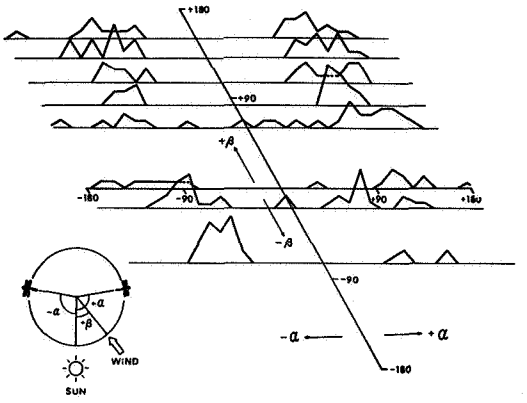

FIGURE 6. Directional dependence on the Sun's azimuth (α) and distributional dependence on wind direction (β). $\beta = \pm 90$ indicates that observation was made when the wind was blowing at right angles to the Sun, causing dragonflies to face almost upwind or downwind to orient to the Sun. Windward sides (right upper quarter and left lower quarter) contain more insects. Number of insects in each point is normalized.

tween these two factors, particularly if one considers that the wind tends to prevail in one direction (SE in this locality at this time of the year). In figures 6 and 7, it is shown that only the distribution of the number of individuals facing either windward or leeward is modified by the wind; there appears to be no direct modulation of the orientation.

The results lead us to conclude that the orientation of the dragonflies, when they are settling on an object that gives them rather unobstructed views of the Sun and sky, will be in a direction close to 98 deg from the azimuth of the Sun. The direction of the wind appears to have no determining influence on the dragonflies' orientation. However, indirectly and secondarily the wind direction affects the number of the individuals in the two halves so that more individuals will face windward than leeward.

Sun and/or Polarized Sky Light

Directional phototactic orientation of many kinds of animals is attributed to the specially developed ability of the animals for the perception of the plane of the polarized light (refs. 10 to 12, 20 to 22, 23 to 26). A question arises immediatley whether this orientation is one of this category.

Two kinds of field experiments were performed in this regard. First a sheet of polaroid film of 20 by 30 cm was carefully brought over the alighting individuals and placed to occlude the sky. Then the sheet was rotated in either direction to cast the different planes of the polarization to the animals. Despite the difficulty in not startling the animals and making them take wing, 30 individuals were tested without inducing any change in orientation. Secondly a mirror was brought to various positions around the animals to cast the rays of the Sun from different directions while they were covered with a shade to obstruct the direct sunlight but leave the sky visible.

Among 30 trials, 22 individuals responded to the converted direction of the Sun and assumed new orientation exactly in the same

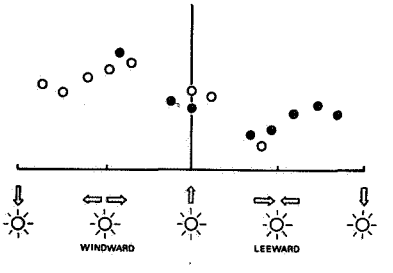

FIGURE 7. Distribution of insects relative to wind direction. Wind direction measured as an angle from the Sun's azimuth. Number of individuals facing easterly in white circle and westerly in filled ones. Largest number of insects alighted in windward sector (middle portion of left half).

manner as with the natural Sun (fig. 8A). There appeared to be two prerequisite factors to induce the reorientation: (1) the converted Sun should shine on the frontal part of the animal's head, since the light cast from the side or more caudal to it could not induce the reorientation; and (2) the animal should have just alighted or, if resting with the wings horizontal or slightly drooped, should be just barely startled.

Although much detailed study should be executed, the direction of the Sun appears to be primarily determining the orientation. However, we could not exclude at present the possibility that the polarization plane perception may play a role.

Experiment with Rotating Stick

A stick was raised vertically so that it could be rotated slowly around its long axis and placed in the middle of the bamboo sticks on which the observations were performed (fig. 8B). When the dragonfly came to rest on top of the stick, the stick was rotated slowly in either direction. The animal remained stationary so that it rotated in the same direction as the stick up to a certain degree; then it suddenly regained its orientation relative to the Sun by stepping around. This same procedure was repeated intermittently while the stick was rotating. We have not yet been able to obtain a definite figure for the minimum deviation which triggers the reorientation in this manner, because of variations due to the slight vibration or wind, both of which also appeared to trigger the reorientation. Sometimes the animals were rotated more than 90 deg from the original orientation so that they faced toward or away from the Sun. These animals oriented in relation to the azimuth of the Sun actively through the shorter of the two possible routes.

Ocellar Contribution

The contribution of the ocelli to the dorsal light response of the dragonfly *Anax imperator* (ref. 13) and the phototactic turning tendency of the locust *Locusta migratoria* and the cricket *Gryllus bimaculatus* (ref. 27) has been reported. Our observations show that the reorientation induced by the conversion of the Sun appears to occur only when the light falls within about 90 deg from the front, which is quite close to the lateral extent of the receptive field of the well developed frontal ocellus as determined by electrophysiological method. Therefore, we have attempted to elucidate the possible contribution of the ocelli, particularly the frontal one. More than 100 dragonflies were collected, and both their frontal and lateral ocelli were either painted black or cauterized. Then they

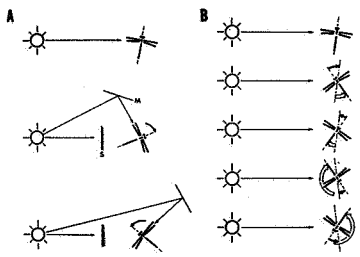

FIGURE 8. (A) Reorientation of the dragonfly induced by change of Sun's direction with a mirror. Upper: normal orientation. Middle and lower: either clockwise or anticlockwise turn of dragonfly is induced according to altered Sun's direction. Animal will face almost in right angle (98 deg) to new direction of Sun. *M*: mirror. S: shade. (*B*) Reorientation of dragonfly induced by rotation of the stick on which animal is alighting: Uppermost: normal orientation. Second and third: reorientation (black arrow) with small angle rotation of stick (white arrow) in either direction. Fourth and lower: reorientation with rotation of stick in large angle (more than 90 deg). Dragonfly chooses smaller angular movement to take a new orientation, which is also almost at right angles to Sun's direction.

were put into a cage of 5 by 10 by 3 m with finely meshed net. The cage, standing in the open air close to the experimental field, contained bamboo sticks to provide proper alighting places and the dragonflies were permitted to fly freely in the cage. All the ocellus blinded insects showed quite unpredicatable behavior. The majority of them perched vertically on the surrounding net after a considerable period of jerky flight. In addition, the compound eyes of only one side were blinded in a number of insects before they were released in the cage. Since no individual was seen to behave normally in these cases, it is impossible to say at present whether the ocellus contributes to the orientation. More disturbing is the fact that it was difficult to induce the normal individuals to rest on the tips of the bamboo sticks as long as they were caged, although the mesh of the surrounding net, at least to the experimenter, does not appear to be an obstruction and the cage communicated freely to the outside through the net.

LABORATORY EXPERIMENTS

A number of basic questions still remain unsolved: (1) What is the essential attribute of the stimulus to determine the orientation, i.e., polarized light and/or the Sun itself, although the field observation points toward the latter?

(2) Which sensory organ or organs are mediating this orientation?

(3) To what extent is the orientation related to the dorsal light reaction already reported?

(4) Is this a new type of transverse orientation?

To answer these questions, it should be quite helpful (or, in fact, sometimes compulsory) to have the dragonflies behave in the laboratory as they do in the field. Unfortunately all attempts to date to induce their orientation in the laboratory have proved to be futile. However, in some of the attempts, a number of interesting properties are revealed and will be noted here.

Freshly collected dragonflies were brought into a net cage in the laboratory. The top of the cage was either covered with a transparent or translucent plastic ceiling. A number of sticks were also provided to simulate the alighting positions. Various conditions of illumination were tried without avail. Spectral content of light source, amount of polarization, illumination intensity, and the direction of the illumination were considered. Also the speed of the air current was varied to simulate the wind. Under all these conditions or their combinations, the animals were seen either to take a night perch posture on the side of the stick or on the wall of the cage, with the tail down vertically, or to fly incessantly in a positive phototactic direction toward the light source. Quite interesting was the fact that when the animals were freed in the laboratory where the whole series of artificial light sources were lighted simultaneously, animals were seen to dash toward a small glass window with a closed pane facing the northern sky which was far less bright than was the light from the lamps. Although a few insects were attracted first to the artificial lights, they actually oriented almost immediately to the sky light.

Some animals were tethered, provided with a rotating disc under their legs to measure their turning tendency, and illuminated from the side. The observed responses were clearly of the dorsal light reaction and not of the orientation described in this paper. Of interest again is the fact that the insects under resting conditions did not respond even to the unilateral illumination of quite high intensity. However, a small vibration of the substratum or a weak air puff brought the animal to an

alerted condition. When this was done simultaneously with the side illumination, the insect turned the upper part of its head toward the light source and at the same time showed a torque which was developed by the leg movement to face the light source. Wings were removed from some insects which were then freed on the table and various illuminations were applied. No comparable part of the orientation observed in the field was brought out in these cases except the sign of the dorsal light reaction.

It is worthy to note that the dragonfly operates with discrete levels of activity, and the responsiveness of the individual is solely dependent on which level of activity the animal is in. The levels are tentatively divided into four: (1) complete resting level while alighted, particularly during night perching; (2) semi-alerted level, with visual system activated, and oculomotor activity; (3) flight perparatory level, with more sensory systems involved; (4) flight level, with sensory systems in full operation and flight muscles in action.

SPECULATIONS AND DISCUSSION

Light Compass Reaction

The observed orientation agrees with the ordinary light compass reaction in three major ways:

(1) The reflected sunlight from the mirror can induce a change in the direction of orientation so that the reflection of the Sun comes to occupy the direction previously occupied by the Sun itself. This is the classical experment which Santschi (ref. 28) performed on the ant where he found that the Sun directed the ant along its track.

(2) The dragonfly orients in a fixed angle to the direction of the Sun, in a manner of transverse orientation (ref. 29).

(3) The insect turns into new orientation with as little turning as possible and thus chooses the shorter route to reach one of two possible directions. This agrees well with the responses of a number of insects in their light light compass reactions which are described by v. Buddenbrock (ref. 30).

In two aspects, however, the orientation described here does not exactly fit the normal definition of the light compass reaction. Namely (1) the animal is not in locomotion to show the directional orientation although there are some indications that the flying dragonfly also orients relative to the Sun, suggesting that the same orientation mechanism is operative in the insect on wing; and (2) the orientation angle with the Sun is not variable as in the ordinary light compass reaction; i.e., the angle appears to be predetermined innately.

These two different characteristics may indicate that the orientation described here may be a different entity than the light compass reaction.

Possible Ecological Values of Orientation

In early autumn enormous numbers of dragonflies belonging to the *Sympetrum* species can be seen flying in one direction particularly in early morning and late afternoon hours. Casual observation definitely shows the direction of the flight is also at right angles to the azimuth of the Sun and almost unidirectional. Swarming is more common in a gentle breeze and is not observable on windy days. Although these points should be defined more quantitatively to prove their existence more definitely, the orientation during the flight at present seems to be governed by the same factors as in the alighting individuals.

If this is proved to be true, a significant contribution to the understanding of the migratory behavior of the dragonfly will have

been made. Assuming the increase in their flight activity after sunrise and close to sunset, and also assuming a prevailing tendency of the wind to blow from only one direction at a certain time of the year at a given locality, northsouth movement or reported appearance of the southern species in north can be readily explained.

Another significance of the orientation may be found in the predatory behavior. Moving small objects against a neutrally lit background is known to induce the predatory response in many kinds of animals. The orientation found here is consistent with this need because the orientation of right angle to the light source gives more chance to perceive the prey in silhouette against the neutrally lit sky.

Mediating Receptor or Receptors

One of the most interesting features of the orientation described here is certainly the orientation angle to the azimuth of the Sun. The angle is about 8° greater than a right angle, and it is fixed at this angle all day. The inference is that there must be a certain structural basis in the mediating receptor that determines this orientation angle. The migrating locust has been described as taking a right angle orientation to the sun (the sun basking response to maintain the warmth of the body by making a maximum exposure to the sunshine, Fraenkel, ref. 31). There is no mention of the particular receptor to mediate this response, which suggests that the temperature change induced by the orientation is an operating factor. In the dragonfly this explanation appears to be inappropriate because of the short latency of response observed in the experiments with the rotating stick and mirror, and the quick settling to the oriented position immediately after alighting. Also a slight deviation of the orientation angle from due right angle cannot be explained at all.

Visual receptors, i.e., the compound eyes, possibly with some contribution from the ocelli should then appear to be the receptors concerned. At present only possibilities can be pointed out without much proof from the experimental data. First it may not be coincidental that the alignment of the ommatidia on dorsal side of compound eye on one side is not parallel to the other side but forms convergent lines of a little less than 20°. If, and only if, the orientation is operated by the perception of the plane of the polarized light by the side of the sky opposite the Sun (which is known to have the strongest polarized light content), the mechanism is such that the animal aligns the ommatidial array parallel to the plane of polarization in the compound eyes opposite to the Sun. The resultant orientation angle can be expected to deviate in just about the same degree from right angle to the Sun as we observed. However, this speculation seemingly contradicts the findings with the rotating polarizer and the mirror conversion of the direction of the Sun. Certainly much more detailed study under controlled laboratory conditions must be done, particularly on the functional analysis of the polarization sensitivity of the dragonfly eyes, before advancing the speculation further.

Second there might exist a clear demarcation of the functional properties of the area of the compound eye in relation to the induction of the turning tendency in the horizontal plane, as is already proved in the dorsal light reflex (ref. 13). Third there still remains a possibility that the frontal ocellus may determine this angle. Electrophysiological analysis of the receptive field of the frontal ocellus reveals that the receptive angle in the horizontal plane is quite wide and appears to extend little more than 90° on both sides of

the head. However, the ocellus is so sensitive to the light that photoinhibition of the impulses, first described by Ruck (ref. 32) is found to be induced even after the surface of the ocullus is painted completely black. The light falling of the receptor cells through the thinly pigmented frons was found to be enough to produce the inhibition, thus making the definitive determination of the receptive angle difficult. This also suggests that in order to blind the ocellus, extra care should be taken to prevent the light falling through the surrounding cuticle on the receptor cells.

Effect of Wind

There appears to be a simple explanation for the fact that the wind direction results in an uneven distribution of dragonflies. This is probably produced by the difference in stability of hovering over the alighting position. The insect approaching downwind was more likely to miss the landing point than the one flying upwind. The insect approaching the stick usually makes a short maneuvering course correction immediately before landing to align himself with the wind direction. After alighting, the dragonfly will move to take the orientation to the azimuth of the Sun going always through the shorter of two possible routes. The resulting orientation will thus be at almost 98° to the Sun and likely to face windward.

Finally there is no indication of the "clock" concerning this orientation. The orientation angle is fixed throughout the day and not altered or modified according to the time of the day.

Also it is quite disturbing in the laboratory to not know how to induce the dragonfly to behave and orient as it does in the open field. Without this knowledge the experimental analysis, particularly of the operating stimulus and its receptor, appears to be remote. It is hoped that this knowledge will be discovered and we will be able to make the dragonfly obey the command of our artificial sunlight. Until then the true nature of this orientation remains a riddle.

DISCUSSION

WILLIAMS: Have you tried to analyze the effects of temperature, because the orientation that you described will give it maximum heat?

HISADA: Yes, since the temperature factor is known to be effective in the orientation of the locust. I don't think, however, that this is the case in the dragonfly, because (1) partial illumination of even the head only will induce the reorientation and (2) the latency of the response appeared to be too short to be explained by the temperature effect. It may, however, be possible that the biological significance of this orientation lies in the regulation of the body temperature. On a very hot day, I have observed one individual taking a very peculiar posture in which the animal's tail was held upright directly pointing to the sun, thus exposing minimum area of his body to the direct sunlight. This obelisk-like posture may also be pertinent to the temperature regulation.

WILLIAMS: I have noticed that when dragonflies fly close by, you can detect some that are maimed and thus identifiable individuals. It appears after only a few weeks' observation that there is a territoriality in hunting areas during the evening period. Have you noticed this?

HISADA: Territorial behavior is not apparent in this species, although many other dragonflies are known to have territorial behavior.

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When the Beachhopper Looks at the Moon: The Moon-Compass Hypothesis

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THE DISCOVERY BY VON FRISCH AND KRAMER that honey bees and starlings are able to use the position of the Sun to orient in a fixed compass direction seemed highly improbable when initially described. Subsequent research, however, has borne out these claims and demonstrated that many other animals, both vertebrate and invertebrate, have the same capacity. Sun-compass orientation now represents one of the most secure foundation blocks underlying the hypotheses proposed to account for otherwise unexplainable cases of animal orientation and navigation.

Shortly after this remarkable discovery, two Italian workers, Pardi and Papi, published substantial evidence indicating that crustacean sandhoppers, amphipods of the genus Talitrus, are also able to use Sun-compass orientation, with a directional preference that would be seaward on the beach from which the animals were collected (ref. 1); and advanced the claim, on less extensive evidence, that these amphipods can also use the position of the Moon in order to orient toward the shoreline, in a manner similar to their performance with the Sun (ref. 2). Moon-compass orientation of this sort would be a phenomenon even more remarkable than Sun-compass orientation, because of the complex pattern from hour to hour and day to day in the direction of the Moon. It is surprising, then, that so little subsequent research on Moon-orientation has been undertaken to verify or disprove this claim.

A possible explanation for this lack of interest may be that the Moon-compass hypothesis is an intrinsically unattractive propostion. As applied to talitrids, the hypothesis requires the assumption that the amphipods have two separate and independent timing mechanisms: a Sun-clock, synchronized by the day-night cycle, which the animal consults when orienting by the Sun; and a Moon-clock, which operates at a slightly slower rate, which is synchronized by other environmental stimuli, and which the animal consults when orienting by the Moon. The amphipod would, then, not behave as a temporal unit, with internal synchronization of various functions, but instead must be assumed to have two time-measuring systems, much as a railroad conductor might have two separate watches, one in each pocket, to use when crossing to different time zones. For me, then, the Moon-compass hypothesis is esthetically unappealing.

Nevertheless, I will be presenting extensive evidence that seems to favor the Moon-compass hypothesis. But let me reemphasize at the outset that this is not because I like the hypothesis. The reason for this anomalous position in which I find myself is that there now exists an appreciable body of data on nocturnal orientation of talitrids, data that require explanation. Although the Moon-compass hypothesis is an esthetically unattractive way of explaining these data, it seems to me to be the best of the alternatives presently available.

The evidence bearing on the Moon-compass hypothesis that I propose to review consists of the data from five published papers (ref. 2, hereafter designated as San Rossore I experiments; ref. 3: San Rossore II experiments; ref. 4: La Jolla experiments; ref. 5: Castiglione experiments; and table 1 [1] of ref. 6: Mogadiscio experiments); a manuscript by Peter Craig (Univ. of California, Santa Barbara),[2] which he has very kindly sent to me before publication (Santa Barbara experiments); and the data from two extensive studies of my own that have not previously been published (Naples and Malibu experiments). These latter data are summarized in detail in appendixes A and B and constitute a larger number of experiments than the total contained in all the published literature. I will draw upon all of these data in an attempt to answer a series of questions of increasing complexity about the nocturnal behavior of talitrids.

Methods and Materials

The procedure used in studies of Moon orientation has consisted of collecting groups of amphipods from the beach, usually during the daylight hours, at which time they are buried at depths of 2 to 20 cm into the sand; storing them in light-tight containers until the start of observation (exceptions in ref. 4[2]); placing them into a circular, sealed observation chamber, in which a view of terrestrial landmarks is prevented; and recording their positions—the directions of orientation—as they aggregate around the margin of the container.

About 25 animals have been used per experiment. In all published experiments, the animals have been stored in bottles containing sand; removal of the animals from the sand for transfer to the orientation chamber requires several minutes of exposure to moonlight. In the Naples and Malibu experiments (appendixes 1 and 2), I kept the animals before observation in sealed containers in which there was only a strip of paper towel, moistened with seawater; this permits transfer to the orientation chamber within a matter of seconds after removal from darkness.

Craig and I have photographed the animal positions with the camera above the observation chamber, through a glass cover; Papi, Pardi, and Ercolini have photographed the animals from beneath, or, in one study (some of the Mogadiscio experiments) made visual counts of position. In most cases, the orientation chamber has been heated to about 20° C, and in some cases, also dehydrated; the possible influence of these experimental conditions is discussed in detail in question VII below.

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[1] The other data in ref. 6 are derived from performances when the Moon was passing through the zenith or culminating in the north. The orientations observed were usually widely scattered, with only eight results statistically significant. The orientations also deviated by large amounts from the expected direction, a fact which the authors attribute to peculiarities in lunar path on the equator during the equinox. For this reason data in tables 2 and 3 of ref. 6 may not represent a valid test of the Moon-compass hypothesis.

[2] CRAIG, P. C.: An Analysis of the Concept of Lunar Orientation in *Orchestoidea corniculata* (Amphipoda). In press, Animal Behavior, 1971.

All of my experiments have been conducted in locations far from the possible influence of urban illumination. Apparently only the Mogadiscio experiments were conducted within a large city, and the experimenters, in that case, have described the precautions they took to reduce the influence of urban lighting to a diffuse glow (ref. 6, p. 229).

The direction of orientation of the animals within an experiment has been averaged by a vectorial method (ref. 1, p. 463) that is now widely used in orientation studies. In addition to its direction, this vector has a length that can range from zero to one and measures the internal agreement in the experimental observations, with a short vector indicating a wide scatter in the positions of the animals.

The experimental organisms have included three species of talitrid amphipods: *Talitrus saltator* (San Rossore, Castiglione and Naples experiments), *Orchestoidea corniculata* (La Jolla, Malibu and Santa Barbara experiments), and *Talorchestia martensii* (Mogadiscio experiments). Although these are members of different genera, their morphology and choice of habitat would lead the non-specialist to regard them as very closely related and ecologically equivalent. In my opinion, none of the differences between the data sets to be evaluated can unequivocally be traced to a difference between species; greater differences in nocturnal orientation have been recorded within a species than between species.

SURVEY OF DATA

Question 1

Do the amphipods usually show significant, non-random choices of direction at night when deprived of all obvious orientational clues except the Moon and stars?

A rigorous evaluation of non-randomness in the data from Moon-orientation experiments is a complex statistical problem because all observations have been made with groups of 10 to 40 animals placed simultaneously in a relatively small container. The amphipods often push and crawl over each other, so that their choices of position cannot legitimately be regarded as independent. All statistical tests for the significance of orientation, however, assume a series of independent observations. This disparity between experimental methods and statistical requirements means that the probability levels which can be derived from a statistical test cannot be regarded as completely legitimate; the probability that a given distribution could arise by chance alone may well be underestimated.

In addition, one must be particularly careful about the degrees of freedom applicable to the statistical test, since several of the published sets of data (San Rossore II, Castiglione, Mogadiscio) are derived from repetitive photographs of the same group of animals. A proper, conservative approach requires that the nonrandomness of a particular distribution of directions of orientation be assessed on the basis of the numbers of animals observed and not on the numbers of positions recorded. I have excluded all directions of orientation by talitrids from further data analyses in which a statistical test on the basis of the number of animals used indicates that the orientation was not significantly nonrandom at the 5-percent level[3] or better. (See appendix 3 for a list of published data which have been so excluded.) This precautions seems essential to assure that the data on observed directions of orientation are not

[3] Statistical significance has been evaluated by means of figure 15 of Schmidt-Koenig (ref. 7). Because of the interactions between animals the quoted levels of significance must be regarded as doubtful.

badly distorted by chance factors, or perhaps due only to chance. I have also used only those data from the Mogadiscio experiments which were based on photographs, except when the photographic observation was not statistically significant, in which case I used the data from the succeeding visual count (See appendix 4). This restriction of the usable data is not primarily because of any doubts about the reliability of visual counting of moving animals, but because internal evidence in the data implies that the visual counts were usually made on the same group of amphipods that had just previously been photographed. In that case, the visual counts would not represent independent data in a rigorous sense but only the equivalent of additional photographs of the same animals.

Even after making allowances for all these complications, however, there are sufficient data now available to indicate that talitrid amphipods do, indeed, very often show conspicuous nonrandomness in their orientation at night when they can see the Moon. Table 1 contains a summary of the proportion of experiments in which the observed orientation was strong enough to be considered significant (with reservations; see footnote 3) at the 0.01 level. In several of the experimental series additional cases involved strong suggestions of orientation ($0.01 < p^3 < 0.05$), so that the available data to assess the directions of orientation are somewhat greater than the numbers of cases indicated as positive in this table. The internal consistency of the directions chosen by separate groups of animals, when significant orientation was observed within an experimental series (discussed below), lends further emphasis to the conclusion that nonrandom orientation is involved.

An appreciable number of experiments have been performed, however, in which the observed animal positions are not distinguishable from a random distribution even at the 5-percent level of significance: cases in which the animals scattered in all directions. As suggested by the breakdowns in table 1, animals kept in the laboratory for longer periods of time apparently show random scatter in their directions more often than freshly collected animals; and, as will be considered subsequently, clearer evidence for orientation is often obtained at full Moon than at other times. Nevertheless, there remain many cases —particularly in the data of Craig, but also in other experimental series—in which a scatter not distinguishable from a random choice of directions has been observed and for which no adequate explanation seems available. In

TABLE 1.—*Cases of Non-Random Orientation*

Experimental series	Number of experiments	Percentage of experiments showing strong orientation ($p < .01$) [a]
San Rossore I	16	No data on scatter
San Rossore II		
Freshly collected	17	100
Kept 11 to 20 days	17	65
La Jolla		
Freshly collected	37	89
Kept 1 or 2 weeks	15	47
Castiglione		
Freshly collected	11	100
Mogadiscio		
Freshly collected	34	56
Santa Barbara		
Freshly collected	59	29
Naples		
Freshly collected	25	68
Kept 3 to 10 days	42	57
Malibu		
Freshly collected	44	82
Kept 2 to 5 days	36	72

[a] See footnote 3 in text.

my opinion, the best reply to the question posed in this section is that talitrid amphipods are very often able to orient significantly when they see the Moon, but that they sometimes do not, for unknown reasons.

Question II

Is the Moon the primary orienting stimulus in these experiments, when clear orientation is observed?

The principal evidence available for the conclusion that the amphipods use the Moon for orientation consists of data from mirror experiments: the animals are permitted to view the Moon while they orient; then the view of the Moon is obstructed by a screen, and its image is reflected onto the orientation chamber by means of a mirror from some new direction. Relatively few mirror experiments have been performed, and the results of these tests are not entirely satisfying.

If the Moon is the sole orienting stimulus, one could well expect that the animals would orient toward the mirror with an angle corresponding to that which they assume relative to the real Moon. This has been recorded in some experiments but less convincingly so in others.

The best performance of amphipods in a series of mirror experiments is found in my data for *Talitrus saltator* from Naples (fig. 1A). In these experiments, the mirror sometimes reflected the Moon's image from an altitude of about 30° and in other cases, an altitude of about 60°. Apparently only lunar azimuth affected orientation. Another clearly positive result was obtained in a single experiment with *Orchestoidea corniculata* in my La Jolla experiments (fig. 1B).

Papi and Pardi's results (ref. 2) with *Talitrus saltator* showed a wide scatter (fig. 2A and B), but it is uncertain to what extent these particular results should be a cause for concern, since no data were given on the number of animals used or the degree of scatter within the observations. My results from mirror experiments in the Malibu experimental series also showed large departures from expectations (fig. 2C and D). There was, in these latter experiments, also, a strong trend for the amphipods' orientations toward reflected moonlight to be more dispersed than their orientations toward the Moon itself. All observations included in figure 2C and D are statistically significant ($p<.01$; see footnote 3), but the vector length within the mirror experiments was smaller (i.e., the scatter was greater) than in the preceding control experiment with the Moon itself in 19 cases out of 24.

A single experiment of another sort per-

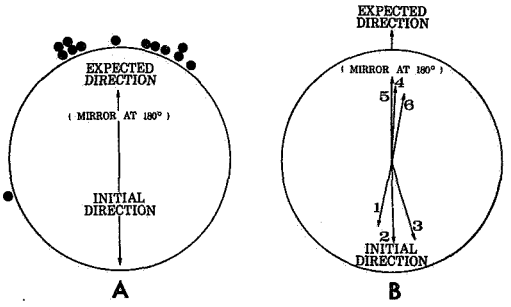

FIGURE 1. "Successful" mirror experiments: (A) Data from Naples experiments, April 3, April 8, and April 13, 1963; direction of orientation initially assumed by the animals has been used for standardization (downward); image of Moon was reflected from a direction opposite the actual lunar azimuth. Each small circle represents orientation observed in a separate experiment; (B) Sequence of observations from mirror experiment of La Jolla series. Arrows represent vectors, lengths of which are proportional to unit radius of the large circle. Numbers refer to sequence in which observations were made; 1, 2 and 3 represent orientation with the Moon visible; 4, 5 and 6 represent orientation to image of Moon reflected from a mirror at 180° from lunar azimuth (after Enright, ref. 4).

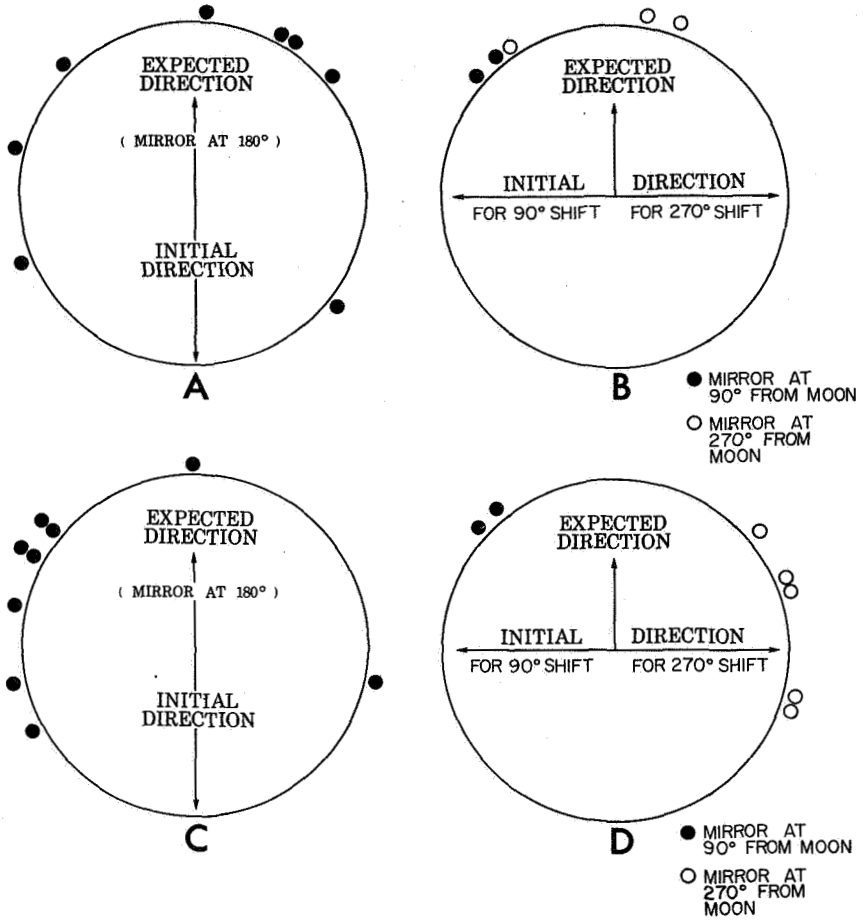

FIGURE 2. Less successful mirror experiments. All orientations standardized relative to initial orientation, so that "expected" direction is upward. Each small circle represents results from a separate experiment. (A) and (B): Data from ref. 2; (C) and (D): Data from Malibu experiments, October 17, 1964.

formed as part of this series seems to me to be of broader significance, and I offer my apologies that this result has not been documented by many repetitions. Following initial orientation with a view of the Moon, and several relatively successful mirror experiments, the animals were left undisturbed in the orientation chamber for 10 minutes, during which time a direct view of the Moon was obstructed, and then their distribution was recorded, still with the Moon hidden. As is evident in table 2, the amphipods which could not see the Moon or its reflection showed strong orientation in a direction not greatly different from that observed when they could see the Moon.

This result was initially very disconcerting; it leads to serious questions about whether moonlight is, indeed, the factor responsible for the orientation. It brought to

my attention, however, the following fact: obstructing a direct view of the Moon by means of an opaque screen 1 m wide located 2 to 3 m from the observation chamber does not provide the animals with a stimulus-free visual environment, any more than it would during the daytime. In addition to the form of the Moon itself, moonlight includes the illumination of a broad region of the sky, and it was very easy to determine the brightest region of the sky, and thereby, the direction of the Moon, under the conditions of the experiment shown in the last part of table 2.

It seems possible, therefore, that the orientation of talitrid amphipods to moonlight does not require a point source of light but can be based on the brightest general region of the total field of illumination. Such an ability might be particularly useful to these animals during night-time orientation on beaches where clouds and fog often partially obscure the position of the Moon.

If this interpretation is correct, then the inconsistent directions often noted during mirror experiments (fig. 2), as well as the shorter vector lengths, would be expected. A mirror experiment would involve exposing the animals to two possible orienting stimuli: skyglow from the real Moon, visible around the edges of the screen; and a point source of light, largely without skyglow, from the mirror.

My own qualitative observations, as well as those of others (ref. 2)[2] suggest that talitrid amphipods are usually disoriented on moonless nights; but as shown in table 1, lack of orientation can also occur, for unknown reasons, on nights when the Moon is visible. Therefore, disorientation on moonless nights —unless it is observed in a very large number of cases—is weak evidence, at best, for the involvement of the Moon in the orientation. It has, in fact, recently been claimed that *Talitrus saltator* can orient significantly both during the daytime and at night, without seeing either the Sun or Moon (ref. 8). The implication of that article is that some unspecified geophysical directional cue, of a category not usually recognized as being biologically effective, was involved. Magnetism was apparently excluded.

It is my opinion that these claims are, at present, insufficiently substantiated to warrant serious concern about the results obtained in Moon-orientation experiments. The published description of experimental methods is extremely brief; it is, therefore, not clear that some accidental aspect of the ex-

TABLE 2.—*Data of October 17, 1964*

Time	Lunar azimuth	Vector length	Orientation azimuth	Angle with Moon
22:59	211°	0.64	156°	−55
23:04	213°	0.74	167°	−46
23:06	[a] 33°	0.89	296°	−79
23:07	[a] 33°	0.93	296°	−79
23:18	[b] (216°)	0.79	171°	−45
23:20	[b] (217°)	0.68	188°	−29

[a] Azimuth of mirror from which lunar disk was reflected onto chamber.
[b] Azimuth of Moon, which had been hidden by opaque screen since 23:06.

perimental arrangement—e.g. cloud pattern, or the light source used for photography, or the slope of the observation chamber (ref. 9) or wind direction (ref. 2)—did not sometimes provide directional stimuli. Beyond this, the statistical test used to assess the results is clearly inappropriate: multiple photographs of the animal positions were used to increase unjustifiably the statistical degrees of freedom, and no allowance was made for possible interaction between animals. Since the reported orientations were much more dispersed than those usually found when the animals see either the Sun or the Moon, concern about subtle artifacts in the experimental situation, as well as about appropriateness of statistical methods, are of extreme importance in evaluating a study of this sort.

While the claim of Van der Bercken et al. remains, in my view, unproven, the lack of complete success in the mirror experiments shown in figure 2 also leaves open the possibility of unknown influences in talitrid orientation. The Moon is clearly implicated as an important orienting stimulus by the fact that reflection of the Moon's image from a mirror produces large deviations from the prior orientation direction, deviations which usually are much greater than would be expected due to chance alone. Nevertheless, it remains possible that some other factor, such as the Earth's magnetic field, also jointly affects the net directions of orientation.

One form of this alternative hypothesis which I have considered and rejected is that the initial orientation is due primarily to magnetism (or a similar clue); that the animals thereafter note the direction of the Moon, and subsequently use the Moon as a reference stimulus. This admittedly rather complex hypothesis might account for the observed inconsistencies in the mirror experiments; the hypothesis predicts, however, that if the amphipods, on their first exposure in the orientation chamber, see the Moon reflected from a mirror, their orientation should be in the same compass direction as that of animals which initially see the unreflected Moon. Subsequent exposure to the real Moon should then lead these experimental animals to orientation in the opposite direction. An experiment which contradicts this prediction is summarized in figure 3.

The net weight of the evidence, in my opinion, supports the assumption that moonlight is the primary and probably only significant orienting stimulus in the experiments which have been performed on Moon orientation. This is, however, probably the weakest link in the chain of evidence leading to the Moon-compass hypothesis. Should convincing evidence become available that talitrids orient consistently in a constant compass direction by means of some subtle non-visual stim-

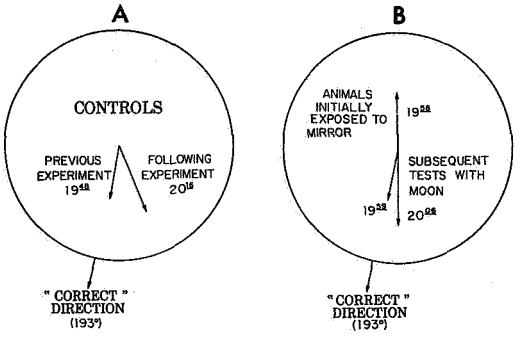

FIGURE 3. Test of hypothesis that initial orientation is based on non-visual stimuli. In these two graphs, north is upward; vector length scaled as in figure 1B. (A) Orientation directions assumed in preceding and following "standard" experiments, with Moon visible; (B) Orientation of animals initially exposed to lunar image reflected from mirror (upward arrow), and subsequent orientation of these same animals, when exposed to actual Moon (downward arrows). Results are compatible with the interpretation that the Moon's image is the only significant directional clue. From Malibu experiments, October 17, 1964.

ulus, then all description in terms of changes in orientation angle with changes in lunar azimuth could be misleading: an artificial but necessary consequence of non-visual orientation in a constant compass direction. Hence, it should be reemphasized that the assumption that moonlight—and nothing else—is responsible for the observed orientations underlies all subsequent discussion.

Question III

Are the directions assumed by talitrids ecologically appropriate, when they orient by moonlight?

It is generally accepted that celestial orientation as shown by talitrid amphipods in an orientation chamber reflects the capacity to return only to the strandline on the beach from which they were collected, and not necessarily to a particular point on the beach. Even an orientation which is within 60° of the "correct" direction would permit animals which had been displaced landward to return to the strandline by covering a distance only twice as great as that necessary by the most direct route; a deviation of 75° would imply a four-fold increase in distance travelled, so only orientation more than about 75° "wrong" would be ecologically useless or misleading.

The data from the various experimental series are summarized in figures 4 and 5, and it is evident that when significant orientation occurred, most experimental series involved performances which were consistently better than the minimum required for the behavior to be ecologically useful. Only in my Naples experiments (fig. 5C) and, to a lesser extent, my La Jolla experiments (fig. 5B), were an appreciable number of the observations in an ecologically "wrong" direction. Craig's observations, for which individual data are not yet available, also involved an apparently faulty choice of directions. He studied animals from three beaches, which faced NNW, SE and SSE, and concluded that when significant orientation occurred (which was seldom—see table 1), "the amphipods generally oriented in the northeast sector, a direction of puzzling ecological significance." Since no breakdown of these observations by beach-of-origin was given, it is conceivable that a major fraction of the observed statistically significant orientations in this study were also within, say, 60° of the appropriate direction.

Within the framework of this question about ecological significance, it seems appropriate to consider briefly whether the usefulness of Moon orientation for the animals under field conditions represents an adequate explanation for its evolutionary origin. It is, of course, true that the Moon would be above the horizon at night no more than half of the month; and that, in coastal areas, nighttime clouds and fog are often common and intense enough that the animals would be unable to perceive or determine the Moon's direction even when it is above the horizon. One must presume, then, that orientation by the Moon is only a supplementary mechanism for direction finding by talitrids on the beach at night, and indeed, other mechanisms have been documented, including orientation to wind direction (ref. 2), and visual orientation to conspicuous topographic features (ref. 10).

Granted that the amphipods may seldom in nature have both the need and the opportunity to use the Moon as a basis for orientation, it nonetheless seems plausible that, at least occasionally, for some individuals in the population, the capacity may have a major influence on survival. The persistence, through evolution, of a given behavioral pattern does not require that the behavior regularly be used by all members of the population, nor even that the behavior be used oc-

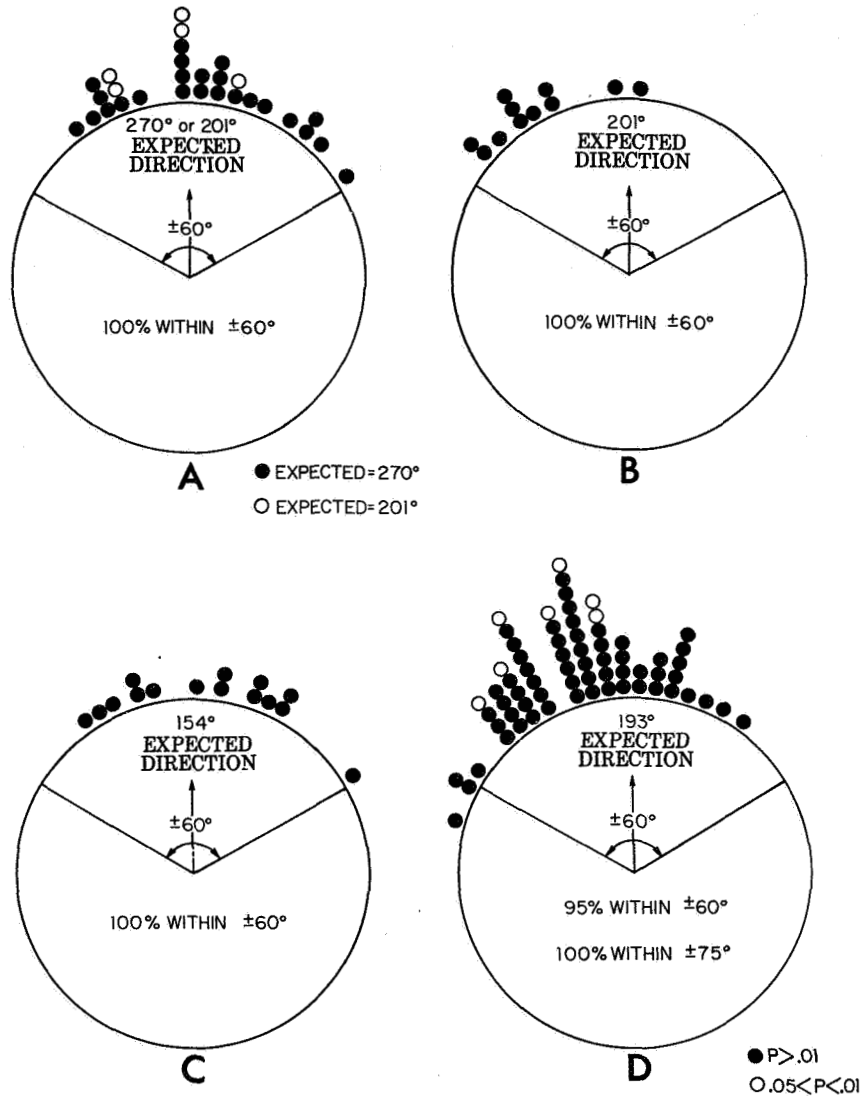

FIGURE 4. Best results for ecological appropriateness of lunar orientation. "Correct" direction (i.e. toward sea on beach of origin) is upward in these graphs as well as in figure 5. Each small circle represents results from a separate experiment; solid circles represent results statistically significant (with reservations—see footnote 3 in text) at the 0.01 level; open circles, at the 0.05 level. (A) Data from ref. 3; (B) Data from ref. 5; (C) Data from ref. 6; (D) Data from Malibu experiments (Appendix 2).

casionally by each individual. Even occasional use of the capacity by a fraction of the population would be sufficient to maintain the appropriate genes in the population, provided that the survival value of the behavior, when utilized, were sufficiently great. It

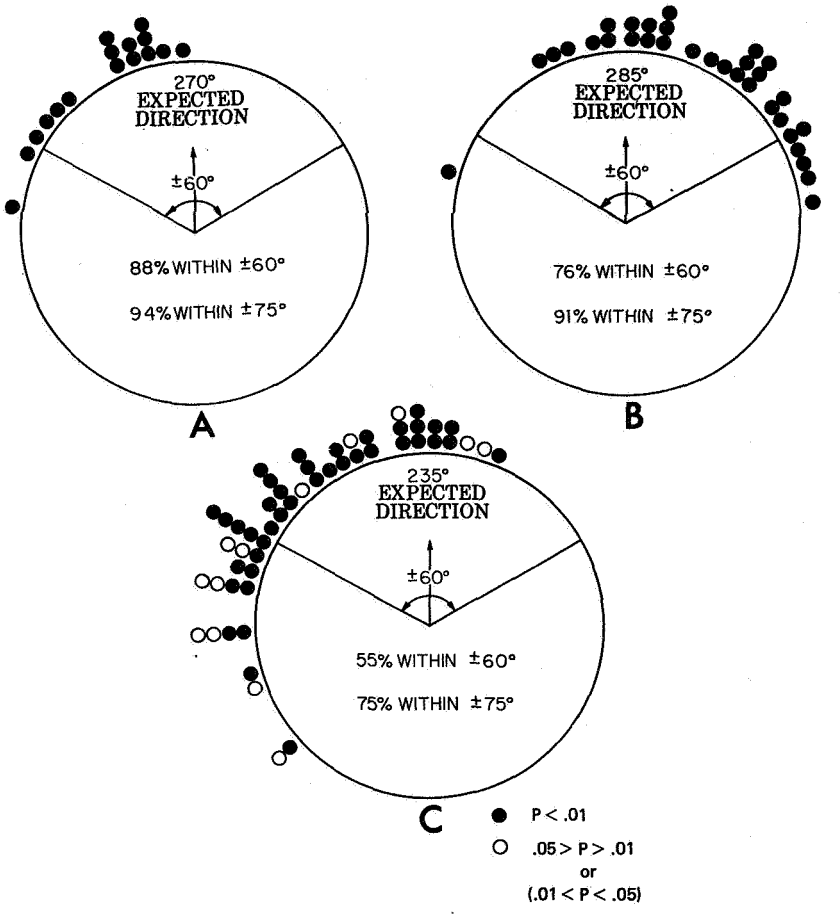

FIGURE 5. Less convincing results for ecological appropriateness of lunar orientation. Symbols as in figure 4. (A) Data from ref. 2; (B) Data from ref. 4; (C) Data from Naples experiments (Appendix 1).

would be an oversimplification of evolutionary processes to argue against the plausibility of Moon-compass orientation only because it would not always be adequate to meet the needs of the animals.

Question IV

Does the lunar orientation of talitrid amphipods involve the capacity to orient in a "correct" direction, regardless of the position of the Moon?

This question is of particular interest for the physiologist concerned with a mechanism; it embodies the essence of what would normally be understood as Moon-compass orientation: the process of time-compensation for lunar movement. Except in the tropics, the amphipods could, in principle, orient to within about 90° of the ecologically correct direction, by means of a non-compensatory, fixed angle of orientation to the Moon, provided that the fixed angle chosen were correlated with the orientation of the home beach. The results shown in figures 4 and 5 could

conceivably all be due to such a non-compensatory orientation.

Contrary to my previous interpretation (ref. 4), it is now my opinion that the question of time-compensation in talitrid orientation must be answered with a qualified affirmative. The qualifications are the following: one must accept the assumption that the Moon is the only orientational stimulus leading to the performance (See Question II, above.); and one must grant that, for reasons as yet undetermined, the animals sometimes fail to show their full orientational capacity. Talitrids are sometimes able to compensate in their orientation for changes in the direction of the Moon, but they do not always do so.

Consideration will be given in a later section to the various factors, including duration of captivity and lunar phase, which do or may influence the performance of talitrids in their Moon orientation. Initially, however, let us ignore such factors and look at the overall results to see whether the amphipods show orientation which varies with position of the Moon. The data are summarized in graphical form in figures 6 and 7. The experiments covered in Figure 6A should be regarded with caution, since it is uncertain which of the results are, as single experiments, statistically significant. In all other cases, the results included in the graphs involved orientation which was statistically significant at the 0.01 level (solid circles), or the 0.05 level (open circles; see footnote 3).

In nearly all experimental series, there are major deviations of the observations from expectations, as is implied, also, in figures 4 and 5. Nevertheless, there is, in each experimental series, a trend toward a smaller angle of orientation as the Moon moves from east through south to west (i.e. lunar azimuth increases). In the results shown in figure 6, the slopes of the regression lines are not significantly different from the expected value of —1.0. In the experimental series included in figure 7, the slopes of the calculated regression lines are significantly different from zero, indicating some compensation; but the slopes are also significantly different from —1.0, indicating that compensation was not always as complete as expected.

An overall view of the data thus demonstrates that the orientation of talitrids to the Moon is not a fixed-angle orientation, but involves time-compensation, which seems in some cases quite complete (figure 6), and in other cases (figure 7) only partial: qualitatively correct but quantitatively insufficient. Even in my Naples experiments, in which the directions of orientation were poorest in terms of beach-of-origin (fig. 5C), the amphipods were, in a significant fraction of the experiments, changing their orientation in an ecologically appropriate direction with changes in lunar azimuth (fig. 7C).

Question V

What is the evidence, based on experiments performed within a single night, that the amphipods change their orientation, relative to the Moon, in the appropriate direction?

True Moon-compass orientation should involve two phenomena: compensation for changes in lunar position during each night, and compensation between nights for changes in lunar position with changes in lunar phase. The mechanism might be the same, but that remains only hypothesis; different kinds of evidence must be examined to determine whether the two phenomena are demonstrable, and both kinds of evidence are intermingled in the graphs of figures 6 and 7.

The data which show the clearest evidence for appropriate compensation within single nights are summarized in figures 8 and 9, and include four nights of data from the

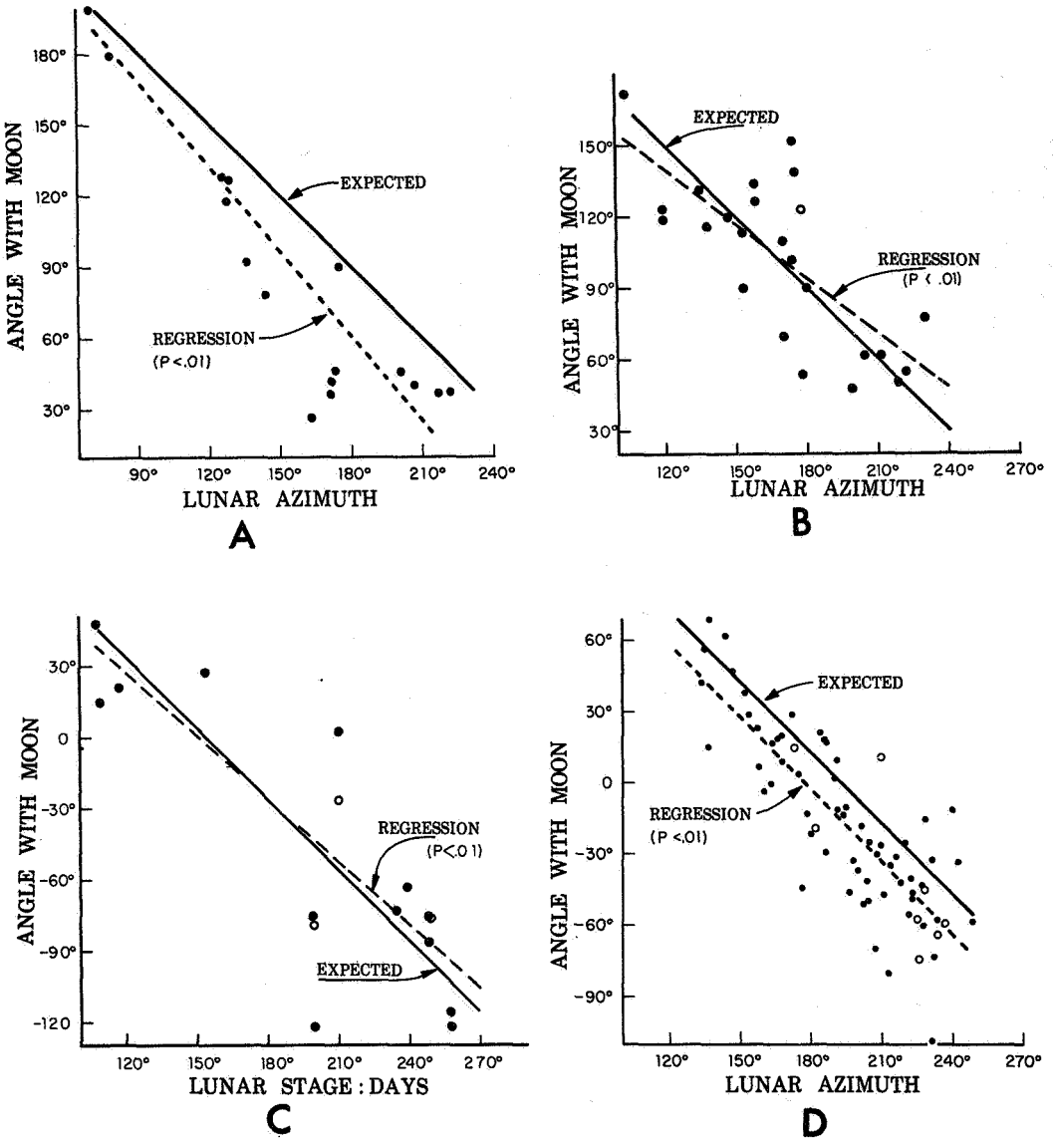

FIGURE 6. Best results showing variation in orientation angle with changes in lunar azimuth. Lunar azimuth measured clockwise from north; orientation angle measured with clockwise being positive. Algebraic sum of lunar azimuth and orientation angle is, therefore, azimuth of orientation, and expected relationship has slope of −1.0. Except in figure 6A, solid circles represent orientation significant (with reservations; see footnote 3 in text) at the 0.01 level, open circles at the 0.05 level. The calculated least-squares regression lines all have slopes which are significantly different from zero ($p < 0.01$) and slopes which are not significantly different from −1.0 ($p > 0.10$). (A) Data from ref. 2; (B) Data from ref. 3; (C) Data from ref. 6; (D) Data from Malibu experiments (Appendix 2).

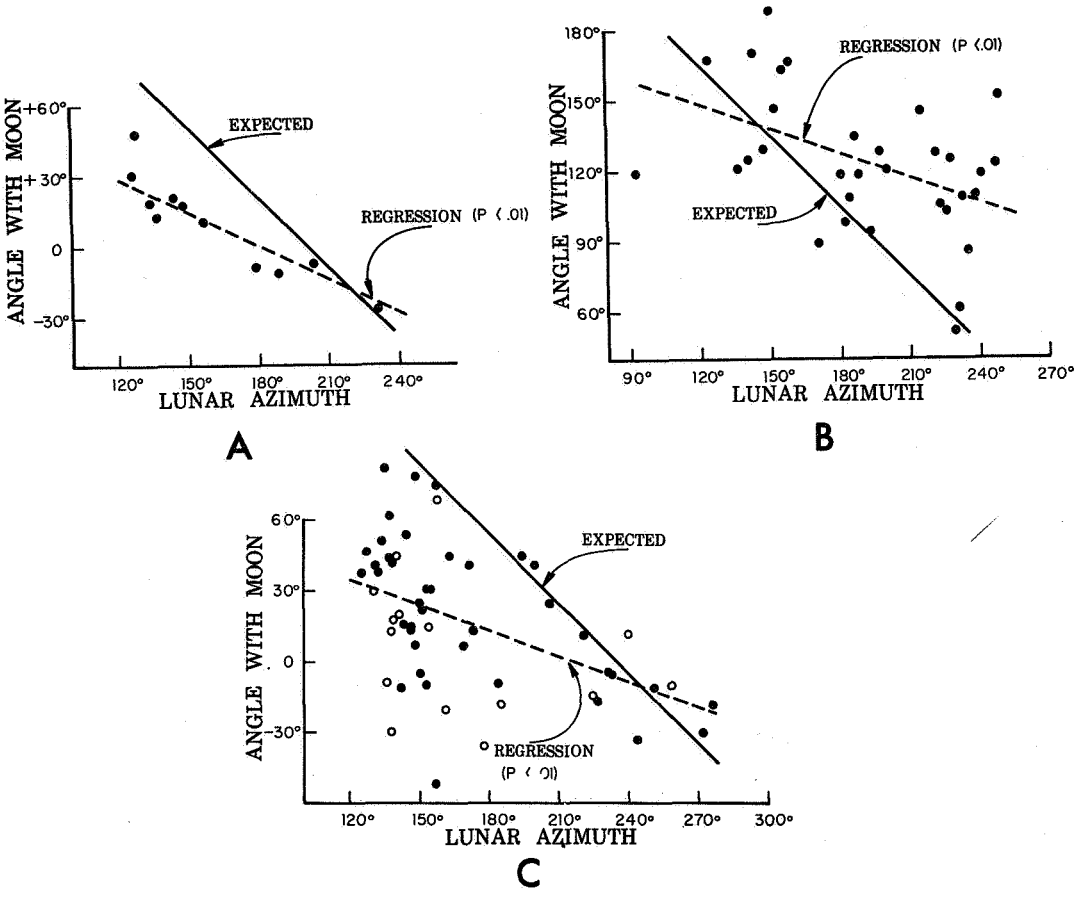

FIGURE 7. Poorer results showing variation in orientation angle with changes in lunar azimuth. Calculated regression lines all have slopes which are significantly different from zero ($p < 0.01$), but that are also significantly different from the expected value of -1.0. See figure 6 for all other details. (A) Data from ref. 5; (B) Data from ref. 4; (C) Data from Naples experiments (Appendix 1).

Mogadiscio experiments, with two to six observations per night (fig. 8A); one night of data from the La Jolla experiments, in which at least two of the treatments ("natural light" and "redarkened", fig. 8B) produced significant trends; and three nights of data from my Malibu experiments (fig. 9A, B and C). In these latter data, the changes in orientation angle are so unmistakable that it would be superfluous to perform a statistical test. It is perhaps surprising, but probably only a coincidence, that the best data for time-compensation within single nights include no data from *Talitrus saltator,* the species which has been most extensively studied for Moon orientation.

Somewhat less convincing data are summarized in figure 10; four nights, with no more than four observations per night, from the Castiglione experiments with *T. saltator,*

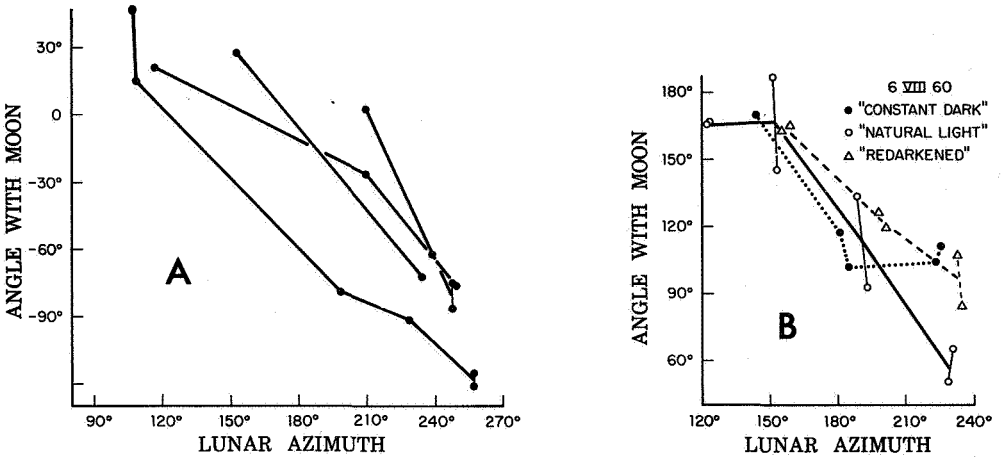

FIGURE 8. Good results showing compensation for changes in lunar azimuth within sets of experiments conducted during single nights. Symbols as in figure 6. (A) Data for 4 nights from ref. 6; data for different nights connected by separate lines. (B) Data for one night, with three different treatments of animals; see ref. 4, for details of treatment.

(fig. 10A), in which trends toward decreasing angle seem evident, but with slopes decidedly less than —1.0; and data from three nights in my Naples experiments, again with *T. saltator* (fig. 10B, C and D), in which there was such large scatter between experiments that none of the calculated regression lines is significantly different from zero at the 0.01 level.

Data from two additional nights of my Naples experiments are presented in figure 11A, and data from two nights from my La Jolla experiments are presented in figure 11B. In these cases, there was no evidence whatever for consistent changes in orientation angle during the night although changes of up to 85° should have been expected. Figure 11C, which is based on eight sets of experiments with *T. saltator* in the San Rossore II series, indicates that in these experiments, also, there was no consistent trend for the animals to compensate within single nights. Finally no evidence for or against compensation within single nights can be derived from the San Rossore I experiments. Within a single night, the largest change of lunar azimuth between observations was 10°, so the expected changes in orientation angle are too small to be detectable.

In summary of these data, then, the evidence is unequivocal that talitrid amphipods have, in some experimental series, shown changes in orientation angle relative to the Moon during a single night, even when maintained in complete darkness prior to observation. These changes involve approximately appropriate compensation for changes in lunar azimuth. In my opinion, however, the evidence is equally clear that the animals do not always show this capacity (fig. 11A, B and C). The reasons for these failures are at present unknown, but various possible experimental complications will be considered in a subsequent section.

Question VI

Are the amphipods able to compensate in their orientation for day of the lunar month?

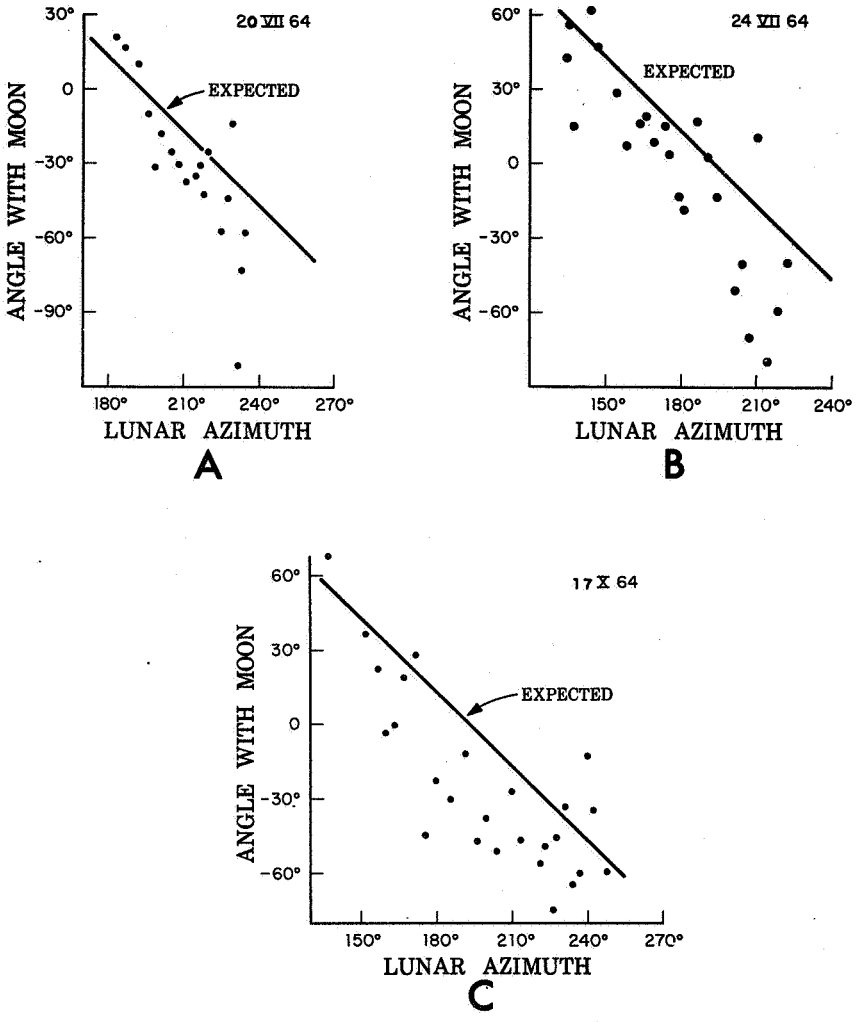

FIGURE 9. Good results showing compensation for changes in lunar azimuth within experiments from single nights. Symbols as in figure 6. Data from Malibu experiments (Appendix 2). (A) July 22, 1964; (B) July 24, 1964; (C) October 17, 1964.

This question involves a critical property by which Moon orientation differs from Sun orientation; because the Moon rises about 50 min later each night, the appropriate angle of orientation, relative to the Moon, changes not only from hour to hour but, for a given hour, changes from night to night. It is conceivable that the amphipods might use some variant of the 24-hr endogenous rhythmicity, which is presumably responsible for Sun-compass orientation, in order to accomplish changes in orientation angle during the night; the "successful results" of figures 8 and 9 could easily be described by a change in angle of 15° per hour such as is implicit in Sun orientation. Such a mechanism could not

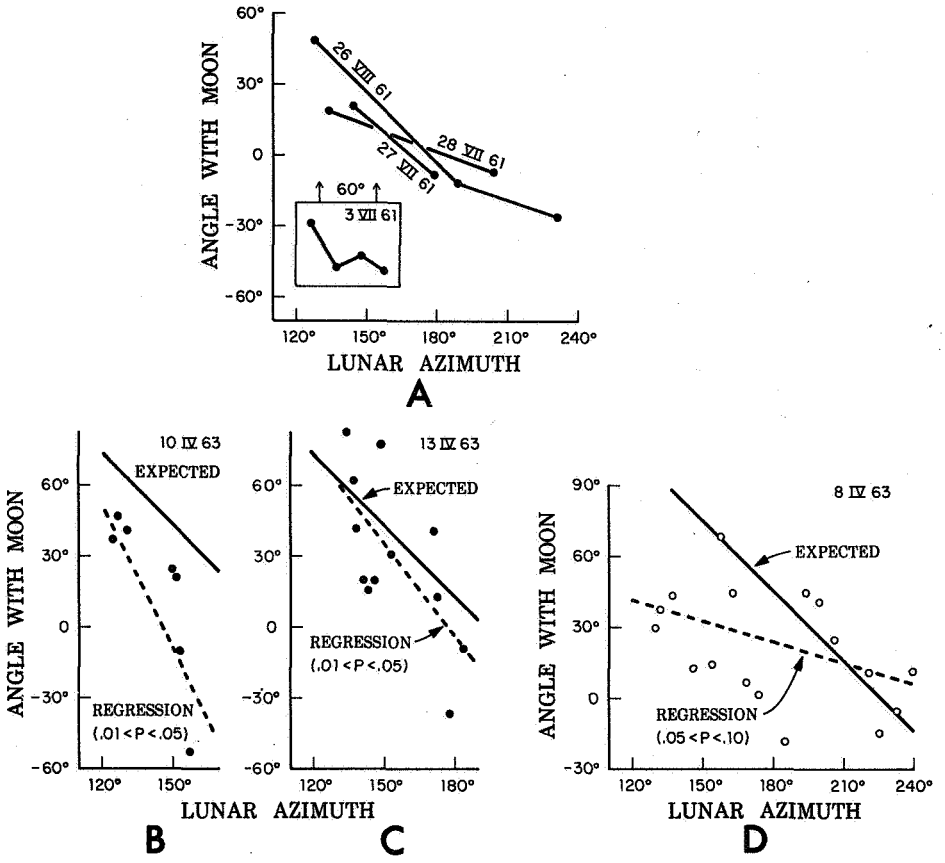

FIGURE 10. Less convincing results, suggesting some compensation for changes in lunar azimuth within experiments from single nights. Symbols as in figure 6. (A) Data from ref. 5; the trend toward negative slope does not seem to approach the expected value of −1.0; (B), (C) and (D): Data from Naples experiments (Appendix 1). None of calculated regression lines has a slope significantly different at 0.01 level from zero, although trends toward negative slope are evident.

account, however, for changes in orientation angle from night to night.

The question posed can best be answered by examining whether the angle of orientation for a given time of night varies with phase of the Moon. Such an analysis requires observations made at comparable times of night, on nights of a different stage in the lunar cycle, a requirement which greatly restricts the usable data. My Malibu experiments involved only two phases of the Moon, which differed by only 4 days, so the difference in orientation angle, for any time of night, is only about 50°. Nevertheless, these data provide striking evidence (fig. 12) for differences in orientation angle at comparable times of night. There is some slight overlap in the observations at different lunar phase, but it seems unnecessary to perform statistical tests to convince even the skeptic that the differ-

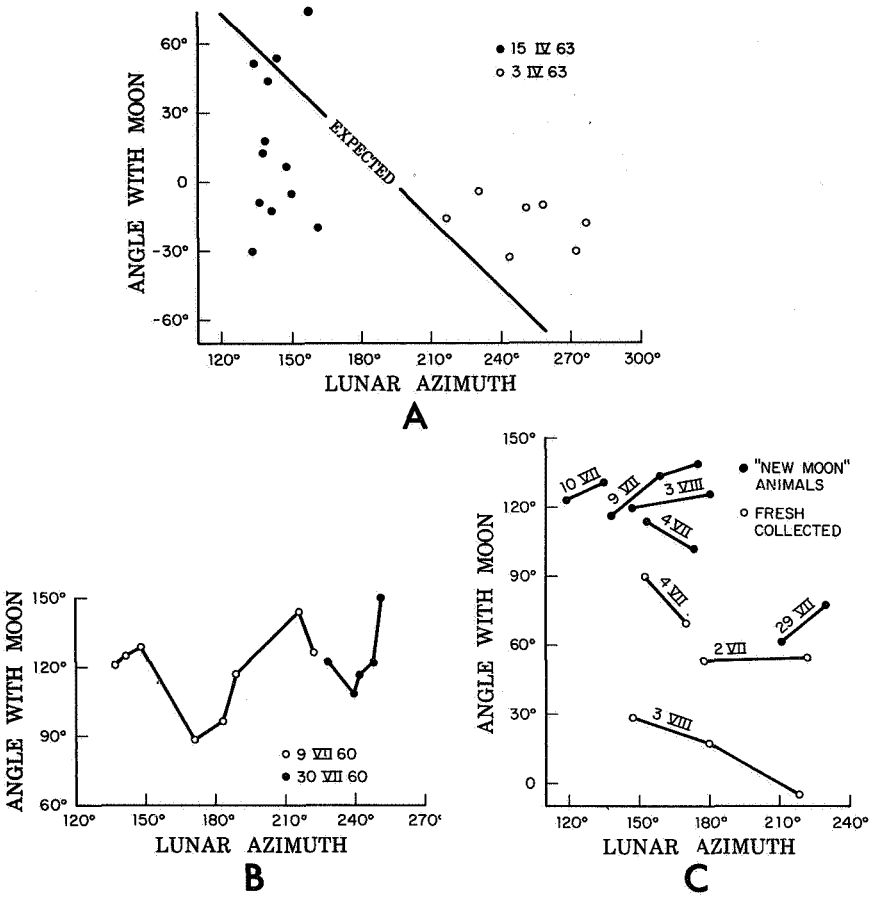

FIGURE 11. Results showing no consistent compensation for changes in lunar azimuth from experiments during single nights. Symbols as in figure 6. (A) Data from two nights of Naples experiments (Appendix 1); (B) Data from two nights, from La Jolla experiments, ref. 4; (C) data from ref. 3.

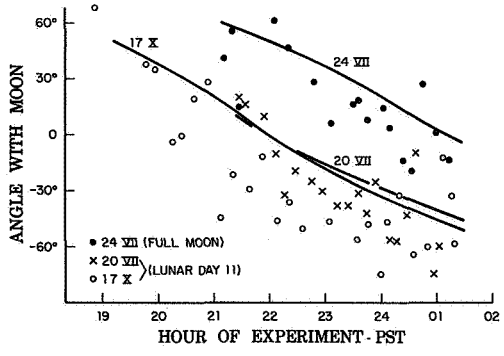

FIGURE 12. Orientation angle as a function of time of night, for different lunar phases: Malibu data (Appendix 2). July 20 and October 17 data for lunar day 10; July 24 data for lunar day 14 (full Moon). Lines represent "expected" orientation on the respective nights. Note that observations on July 24 involve larger angles with the Moon at comparable times of night.

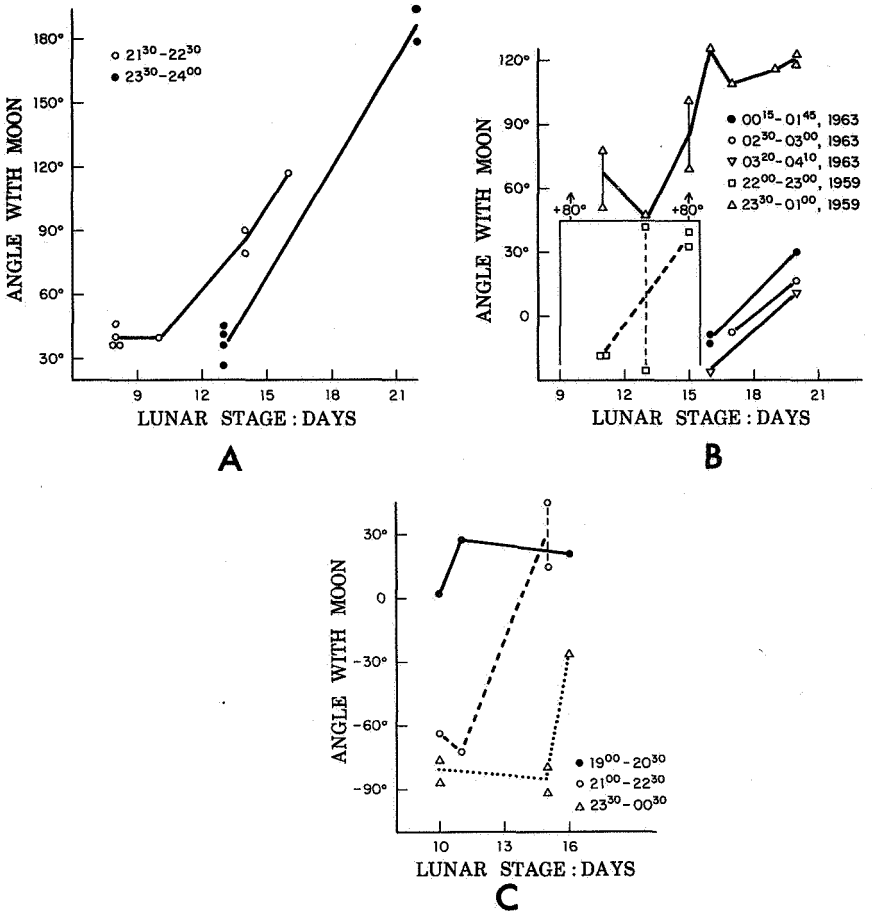

FIGURE 13. Orientation angle as a function of lunar phase, for different times of night. "Correct" compensation should involve an increase in angle of about 12° per day, on the average. (A) Data from ref. 2; (B) Data from ref. 3 and ref. 5; (C) Data from ref. 6.

ence of 4 days in lunar phase was correlated with consistent hourly differences in orientation angle relative to the Moon.

Another type of graph is presented in figures 13 and 14: the data have been grouped according to time of night, and the angle of orientation is plotted against lunar phase. Figure 13 includes data from three studies of *Talitrus saltator* (fig. 13A and B) and one study of *Talorchestia martensii* (fig. 13C); Figure 14 is based on the data from my Naples experiments, also with *Talitrus saltator*. On the average, the expected change in orientation angle in these graphs should be an increase of about 12° per day.

The data clearly show trends in the appropriate direction, some of which are convincing, others less so: for a given time of night, the orientation angle was usually greater during the latter part of the lunar cycle, although the scatter was often very large. Again, even my Naples experiments,

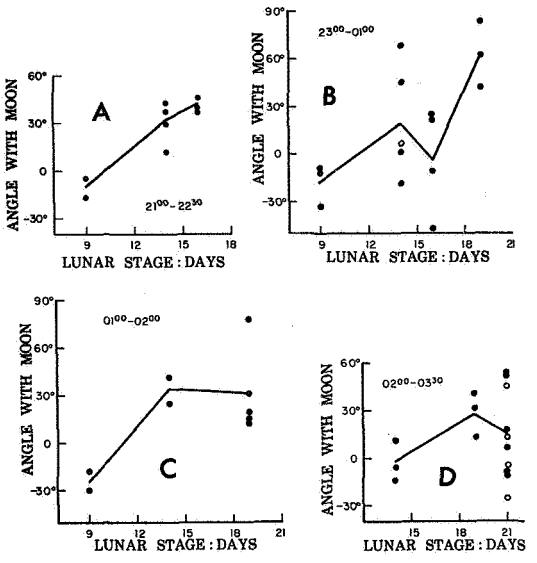

FIGURE 14. Orientation angle as a function of lunar phase, for different times of night. Data from Naples experiments (Appendix 1).

which, on the basis of ecological considerations might be considered largely "unsuccessful" (fig. 5C), showed relatively consistent evidence for conformity to this expected trend (fig. 14).

At the very least, a simple daily rhythm seems completely inadequate to account for the data as presented in figures 12, 13, and 14. The amphipods seem able to compensate to some extent for changes in day of the lunar cycle.

Question VII

What experimental factors might account for some of the variability in the Moon orientation of the amphipods?

A very serious problem for the interpretation of data on Moon orientation of talitrids is that the performances of the animals are so often inconsistent with or contradictory to the Moon-compass hypothesis. It is my opinion that the sources of this variability are at present largely unknown, although some possible sources deserve detailed consideration.

In a criticism of my La Jolla experiments (especially those of fig. 11B), Papi and Pardi (ref. 5) attempt to explain the poor performance by emphasizing the fact that I did not heat and dehydrate the air in the observation chamber. It is their contention (refs. 2 and 5) that when talitrids are placed in an orientation chamber at night, the animals initially show a simple positive phototaxis, orienting directly toward the Moon, and only gradually thereafter, during some several minutes, assume the correct direction of orientation, at some angle to the lunar position. It is claimed that the heating or dehydration of the chamber provides the "releasing stimulus" for reorientation away from positive phototaxis.

The initial observations of Moon orientation of talitrids (ref. 2) purportedly required dehydration of the air in the chamber; the documentation for this claim consists of one example (*ibid.*, fig. 7) which is somewhat unconvincing; the initial orientation was purportedly complicated by skyglow from city lights. In a subsequent paper, Papi and Pardi (ref. 3) stated that dehydration of the air is unnecessary, but asserted (without supporting data) that heating the chamber is desirable, a procedure which they substituted for dehydration in all subsequent experiments. It should be noted, however, that some relatively successful experimental observations have been made without either drying or heating the observation chamber artificially (fig. 8B), and some experiments in which the observations depart very markedly from "expectations" were made in a chamber in which the air was both heated and dehydrated (Naples experiments, fig. 10B, C and D; and fig. 11A) or at least heated to 20°C (data of Craig); footnote 2.

My own data lend very little support to the interpretation of Papi and Pardi; neither the initial positive phototaxis, nor consistently more correct reorientation after exposure to "releasing stimuli" can be well documented in the data. In the La Jolla experiments, the published data are based on animals which were photographed during their first minute in the orientation chamber which was neither heated nor dehydrated. Both on nights of "poor" performance and of "good" performance, the initial angle of orientation averaged about 120°, a radical departure from positive phototaxis. The smallest observed angle of orientation, relative to the Moon, was more than 50° away from positive phototaxis.

In my Naples and Malibu experiments, the amphipods were removed from their darkened containers, rapidly placed in the orientation chamber (which was heated and contained $CaCl_2$ to dehydrate the air) and their positions were then photographed within one minute of their initial exposure to moonlight. The animals were then left undisturbed for 5 min, and a second photograph was taken. The difference between initial orientation and that after 5 min showed an overall trend toward greater angles with the Moon after 5 min, such as might be expected if the animals were becoming less positively phototactic. The differences were, however, usually very small (table 3), and may represent an effect of the photographic lighting which accompanied the first photographs, such as is discussed below under the consideration of multiple photoflashes. Furthermore, the initial orientations were generally consistently different from simple positive phototaxis. The animals tended to orient initially at some angle with the Moon, an angle which then, more often than not, tended to become slightly larger.

In terms of ecological considerations, it also seems surprising, to say the least, that heating to temperatures greater than 20° C and/or dehydration of the atmosphere would

TABLE 3.—*Changes in Orientation During 5 Minutes in Chamber*

Experimental series	Date	Number of cases with:		Median change [a] (deg)
		Greater angle [a]	Smaller angle [a]	
Malibu	July 20–21	15	4	+5
	July 24–25	8	12	−4
	Oct. 17–18	17	8	+6
	Total	40	24	
Naples	April 3–4	3	4	−1
	April 8–9	6	7	−4
	April 10–11	5	2	+3
	April 13–14	10	3	+16
	April 15–16	8	4	+2
	Total	32	20	
	Grand Total	72	44	

[a] Numbers of cases and angle values in this table are based on the difference between the absolute value of the initial angle with the Moon and the absolute value of the final angle.

be necessary for talitrids to use lunar orientation correctly. Air temperatures greater than 20° C are very seldom encountered at night on temperate-latitude beaches; in many areas where the animals are found, such nocturnal temperatures never occur. Furthermore, the air near the sea is usually nearly saturated with humidity at night.

The contention, then, that either low humidity or an air temperature of at least 20° C is necessary for talitrids to use their Moon-compass orientation seems to imply that the capacity would be largely an experimental artifact: demonstrable only in an orientation chamber which has been artificially heated or dehydrated, but essentially useless to the animals on the beach. This I find difficult to accept on evolutionary grounds.

It may, indeed, be true that talitrids, under some circumstances, initially orient toward the Moon with a positive phototaxis, and thereafter, given certain "releasing" stimuli, will orient in the ecologically correct direction. If so, the contention is poorly documented in the published literature and is unsupported by my own experimental observations; the phenomenon, therefore, should not be considered common, nor invoked as a general explanation for the inconsistencies in the available data.

Since all published experiments of the Italian workers involve orientation of animals which had been 5 min or longer in the orientation chamber, I have used the data from second photographs (taken after 5 min) in graphs of the Naples and Malibu experiments, but data from the initial photographs would not appreciably alter any of the graphs or conclusions. It is probably also advisable to heat and dehydrate the observation chamber in future experiments with lunar orientation of talitrids, but the argument in favor of this procedure must be based on consistent methodology, and not on any demonstration that it will affect the results.

I have proposed (ref. 4) that time-compensation for changes in lunar azimuth may require that the animals experience sunset and/or moonrise on the night of the experiment, but an appreciable body of subsequent data (including my own data in Appendixes 1 and 2) now contradicts that interpretation, which was proposed initially to account for the differences between the data of figures 8B and 11B. The data of figure 8B demonstrate that the prior light regime can modify the orientational performance, but the contention that sunset and moonrise on the night of the experiment are, of themselves, the critical factors in the time-compensation process is no longer tenable. Differences in the performances of the animals in different experimental series cannot, in general, be attributed to this factor.

The experiments of the Italian workers with Moon orientation have usually involved taking a sequence of ten or more photographs of the animals, at intervals of a minute or two, using photoflash. The possibility exists that such a series of light flashes might affect the performance of the animals, and I have published suggestive evidence that this is the case (ref. 4): in two experiments, with ten photographs each, taken within 15 min, the animals significantly decreased their angle of orientation relative to the Moon, from first to last photograph; in one case, by 68°, in the other, by 48°. In a similar set of observations, as part of the Malibu experiments, the animals also decreased their angle of orientation relative to the Moon from the first to the tenth photograph in five cases out of six, with a median decrease of 33°. In another similar series of experiments with *Talitrus saltator* (ref. 5), the animals also decreased their angle of orientation relative to the Moon,

from the first to the last photograph, in nine cases out of 11 (i.e. the animals became more photopositive toward the Moon, although Papi and Pardi apparently did not recognize this trend in their data). In this latter study, however, the changes were all small, with a median decrease of only 7°. Differences in experimental methods may well be responsible for the fact that Papi and Pardi recorded much smaller changes than I. Their procedure of photographing the animals from beneath rather than from above would be expected to reduce greatly the intensity of the light which the animals experience from the photoflash.

In my opinion, it still seems desirable, as I have previously suggested (ref. 4), to make only a minimum number of photographs of the animals' positions, with each group of animals, when using photoflash; this precaution seems particularly important when photoflash is given from above. It should be borne in mind that the additional data obtainable from multiple photographs do not add appreciably to the statistical reliability of the data, since, in my opinion, degrees of freedom should be based on observations from different animals. The performance of the species under a given treatment can be far better evaluated by single photographs of separate groups of amphipods, similarly treated, than by multiple photographs of the same, single group—even if the photoflash were to have a negligible influence. This methodological problem, however, is unlikely to account for a major portion of the inconsistencies in the orientational performances evident in the data discussed here. My own data, which include both good and poor performances, are not based on such series of multiple photographs.

Many of the available data lend support to the interpretation that there is greater internal consistency in the orientations observed of a group of animals at times of full Moon than at first and last quarters of the Moon. The vector length, (which is inversely related to the degree of scatter within an experiment) shows an overall consistent trend toward greater values at full Moon than at other lunar phases. Highly significant differences can be demonstrated in several of the data series (table 4). This trend is, of course, not surprising, since the full Moon provides a much brighter stimulus object than does the Moon at first and last quarters. The trend lends further, indirect support to the conclusion drawn to Question II above, that the Moon is the major factor responsible for nighttime orientation. The lesser scatter of directional choices within an experiment would mean that the average direction observed of the orientation of a group of animals is likely to be more reliably estimated at times of full Moon, but this consideration, also, seems unable to account for a major portion of the inconsistencies in the data available.

On the assumption that the orientation is, indeed, based on position of the Moon, one must also presume that compensation for changes in lunar azimuth is based, in some manner, on an internal physiological timing process. It is, then, to be expected that presumably free-running "internal clocks" should, on the average, show a trend toward deviation from correct orientation when the animals have been kept for longer intervals (in some cases, more than 2 weeks) in the laboratory. There is certainly a consistent trend for the amphipods to be less well oriented (i.e. shorter vectors are observed, implying greater scatter within the group) when the animals have been maintained for several days in the laboratory under constant conditions (see table 1). These decreases ob-

TABLE 4.—*Dependence of Vector Length on Lunar Stage*[a]

Experimental series	Lunar stage (days)	Average vector	Number of experiments	Probability of no difference
San Rossore I	13, 15, 16	0.79	8	
	11, 17, 19, 20	0.62	9	$p<.05$, t test
La Jolla	15, 16	0.66	24	
	8, 22	0.53	13	$p<.01$, t test
Naples	9	0.59	8	
	16	0.71	3	
	19	0.68	7	
	21	0.42	7	$p<.001$, F test
Santa Barbara	14, 15, 16	0.39	32	
	7, 8, 9, 10	0.29	27	$p<.001$, t test

[a] All data are for freshly collected amphipods.

served in vector length would, of course, be expected on the basis of desynchronization of the free-running rhythms of the various individuals within the population.

A question of broader interest, however, is whether there is a consistent trend in the directions chosen following longer laboratory holding of the animals, and it must be admitted that no such trend is evident. The overall impression conveyed by the data is that the average rate of the timing process differs very little from the appropriate value of about 14.5° per hr. This conclusion should, however, be examined in more detail.

Very good performances involving time compensation have often been observed of animals which were collected sometime within the day preceding the experiment (ref. 2; tables 1 and 2 of ref. 3; table 2 of ref. 4; ref. 6; and the July data from my Malibu experiments), although there are some exceptions (table 1 of ref. 4; and parts of my Naples experiments). See Appendix 1. Good orientation was also observed in the Malibu experiments, on October 17 and 18, of animals kept for 2 and 3 days in complete darkness. The only extensive series of "successful" experiments in which the animals had been kept undisturbed in the laboratory for longer than 3 days are the data in table 3 of ref. 3, the relevant parts of which are reproduced here as table 5.

It appears that the simplest interpretation of the data for the animals collected in June is that they oriented with an essentially constant angle toward the Moon; there is no appreciable correlation between observation and expectation ($p>0.50$). Thus, the only data which lend some support to the hypothesis, that talitrids can orient with compensation for changes in the direction of the Moon after prolonged maintenance in constant darkness, are the data from the animals collected in July (four observations shown in the lower part of table 5) only two of which differ appreciably from those of the animals collected in June.

It is my opinion, then, that insufficient data are available to draw conclusions about the long-term precision of the biological timing processes which underlie Moon-compass orientation. Good evidence for the continuous operation of the timing process for 2 to 3 days is available, which can sometimes permit the animals to compensate correctly ($\pm$ about 30°) for changes in lunar azimuth (Malibu

TABLE 5.—*Orientation of Amphipods Collected at Preceding New Moon*[a]

Date of experiment	Days since	Angle expected	Angle observed
	Animals Collected June 19		
July 2	13	92°	123°
July 4	15	117°	114°
July 4	15	96°	102°
July 9	19	132°	116°
July 9	19	112°	134°
July 9	19	95°	139°
July 10	20	151°	123°
July 10	20	135°	131°
	Animals collected July 18		
July 29	11	59°	62°
July 30	11	40°	78°
Aug 3	15	123°	120°
Aug 4	16	90°	126°

[a] Data from ref. 3.

data); and the animals are often not completely disoriented, after 2 to 3 weeks under constant conditions (table 5, and parts of table 1 from ref. 4), but these latter data do not necessarily implicate internal timing processes. A constant-angle of orientation, relative to the Moon, will describe nearly all these data.

CONCLUSION: A WORKING HYPOTHESIS

Because so many contradictions are evident in a comparison of the various experimental series, it seems safe to say that no simple explanation can account for all of the data on Moon orientation of talitrids. I would, nevertheless, in concluding this review, like to propose an hypothesis which is compatible with several of the more interesting aspects of the data. This hypothesis is, in fact, only a minor variant of the Moon-compass hypothesis of Papi and Pardi, and I cannot present the hypothesis with the enthusiastic advocacy of a firm believer. My position is, instead, that this is an unattractive hypothesis which I offer provisionally, in the lack of any better alternatives but with the hope that it will eventually be disproven.

The hypothesis consists of three propositions:

(1) Observed cases of compensation for changes in direction of the Moon are based on an internal physiological rhythm with a period of about 25 hours which can persist for at least several days under constant conditions (also the proposal of Papi and Pardi, refs. 3 and 5).

(2) The zeitgeber for this rhythm may be either Moonlight or some factor associated with the tides (probably the former, in view of the recorded changes in the orientation due to treatments with light), but, in any case, the zeitgeber is not as compelling an

entraining agent as the daily cycle, so that even freshly collected animals, under some field conditions, may not have recently experienced synchronizing stimuli.

(3) If talitrids have been long removed from environmental entrainment, either artificially or naturally, the internal rhythmicity no longer exerts appreciable influence on the angle of lunar orientation; the system deteriorates into constant-angle orientation, with an angle which is determined by the beach of origin, but may be modifiable by lighting conditions.

At least four alternatives to this hypothesis have been proposed:

(1) Van den Becken et al. (ref. 8) have suggested that the amphipods do not, in fact, necessarily rely on the Moon for nocturnal orientation, but instead rely upon some other geophysical directional clue. As discussed previously, this hypothesis seems to me to lack adequate supporting data.

(2) I have previously suggested (ref. 4) that the amphipods might utilize a single-cycle time-compensation process initiated by the stimulus of moonrise. As discussed above, the evidence against this proposal is now overwhelming.

(3) Hoffmann (ref. 11) has suggested that the amphipods might utilize their Sun-compass orientation at night, with corrections applied on the basis of the shape of the lunar disc. The fact that successful mirror experiments have been performed both before and after full Moon (fig. 1A), as well as the fact that good orientation has been observed during a partial eclipse of the Moon (ref. 2), seem to argue against this hypothesis, as does the required visual acuity.

(4) Horridge (ref. 12) has proposed that the animals could utilize their Sun-compass with corrections based on the rate of change of lunar altitude. This hypothesis is apparently contradicted by the fact that in successful mirror experiments, the altitude of the mirror, whether 30° or 60°, had no evident influence on the results (fig. 1A). Furthermore, this hypothesis, as proposed, is even less esthetically pleasing to me than the Moon-compass hypothesis. Even granted the sensory capacity of the animals to recognize, within a few seconds time, the rate of change of lunar azimuth and altitude, the application of a correction based on this information seems to me to be an extremely complicated process.

In my opinion, then, the data on lunar orientation of talitrids which require an explanation (especially fig. 4 and 5) can best be accounted for by the Moon-compass hypothesis, with the modifications proposed above—this, in spite of the fact that the assumption of two independent clocks makes the hypothesis basically unattractive to me.

SUMMARY

(1) Talitrid amphipods, when deprived of all obvious orienting stimuli except a view of the Moon and stars, usually (but not always) show non-random orientations which are internally consistent between replicate experiments.

(2) Reflection of the image of the Moon from a mirror onto the amphipods usually produces major deviations in their directions of orientation, indicating that lunar position is the main, and probably the only significant orienting stimulus in these experiments.

(3) When non-random orientation is observed, the directions of orientation are usually, but not always, ecologically appropriate, that is, in a compass direction which would be seaward on the beach of origin, $\pm 60°$; and are often within $\pm 30°$ of this "correct" direction.

(4) The angle of orientation relative to the Moon changes appropriately, in at least a qualitative sense, with changes in the direc-

tion of the Moon. Some experimental series show close correspondence, and others relatively weak agreement, with inconsistencies between nights, but the changes are statistically significant in all experimental series for which quantitative data are available.

(5) In some cases, the animals have clearly shown appropriate changes in the angle of orientation during series of experiments conducted within a single night, but in other cases, no significant change in the angle during the night has been observed.

(6) In most experimental series, freshly-collected animals have shown some tendency to change their angle of orientation, for a given time of night, from one night to the next in an approximately appropriate manner to compensate for changes in day of the lunar cycle.

(7) Prolonged laboratory maintenance of the animals under constant conditions weakens the tendency for significant orientation to the Moon, and the orientations observed suggest that the capacity of the animals may deteriorate as to the choice of a direction which is at a constant angle from the azimuth of the Moon. Sometimes freshly collected animals show a similar tendency.

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APPENDIX 1

Naples Experiments[a]

Date (1964)	Time (CET)	Lunar azimuth (deg)	Orientation azimuth (deg)	Vector length	Number of animals	Significance level	Days since collection	Lunar stage: days
3 IV	21:41	217	201	0.81	16	.01	1	9
3 IV	22.18	231	227	0.92	11	.01	1	9
3 IV	23:00	244	211	0.63	25	.01	1	9
3 IV	23:30	251	240	0.65	24	.01	1	9
4 IV	00.09	259	249	0.38	25	.05	1	9
4 IV	01:25	272	242	0.53	25	.01	1	9
4 IV	01:58	276	258	0.79	17	.01	1	9
8 IV	21:26	130	160	0.33	22	.05	3	14

APPENDIX 1.—(continued).

Date (1964)	Time (CET)	Lunar azimuth (deg)	Orientation azimuth (deg)	Vector length	Number of animals	Significance level	Days since collection	Lunar stage: days
8 IV	21:36	132	170	0.56	26	.01	5	14
8 IV	21:57	137	181	0.57	27	.01	3	14
8 IV	22:23	146	159	0.6	16	.01	5	14
8 IV	22:53	154	169	0.47	16	.05	5	14
8 IV	23:06	158	227	0.62	9	.05	5	14
8 IV	23:20	163	208	0.50	18	.01	6	14
8 IV	23:37	169	176	0.56	31	.01	5	14
8 IV	23:53	174	176	0.54	20	.01	3	14
9 IV	00:24	185	167	0.43	17	.05	3	14
9 IV	00:50	194	239	0.87	21	.01	5	14
9 IV	01:08	200	241	0.67	22	.01	5	14
9 IV	01:26	206	231	0.63	23	.01	6	14
9 IV	02:20	221	233	0.62	22	.01	5	14
9 IV	02:34	225	211	0.39	23	.05	3	14
9 IV	03:08	233	228	0.39	31	.01	5	14
9 IV	03:39	240	252	0.39	16	.05	5	14
10 IV	22:03	125	163	0.65	26	.01	5	16
10 IV	22:13	127	174	0.66	25	.01	0	16
10 IV	22:28	131	172	0.83	17	.01	5	16
10 IV	23:48	150	175	0.71	15	.01	5	16
10 IV	23:54	151	173	0.75	22	.01	0	16
11 IV	00:02	153	143	0.53	18	.01	5	16
11 IV	00:14	157	105	0.70	22	.01	0	16
14 IV	00:39	135	218	0.74	24	.01	1	19
14 IV	00:47	137	199	0.84	15	.01	8	19
14 IV	00:55	138	180	0.61	21	.01	1	19
14 IV	01:07	141	161	0.44	17	.05	3	19
14 IV	01 18	143	159	0.53	26	.01	1	19
14 IV	01:32	146	161	0.45	23	.01	3	19
14 IV	01:42	149	217	0.72	16	.01	1	19
14 IV	02:02	153	184	0.84	18	.01	8	19
14 IV	02:09	155	186	0.62	23	.01	1	19
14 IV	03:15	171	210	0.72	16	.01	1	19
14 IV	03:24	173	186	0.53	20	.01	8	19
14 IV	03:43	178	142	0.80	6	.05	1	19
14 IV	04:07	184	175	0.50	23	.01	3	19
16 IV	02:01	133	103	0.50	13	.05	0	21
16 IV	02:09	134	186	0.68	21	.01	10	21
16 IV	02:16	136	127	0.37	24	.05	0	21
16 IV	02:24	138	151	0.50	16	.05	3	21
16 IV	02:31	139	157	0.42	19	.05	0	21
16 IV	02:39	140	195	0.39	23	.05	3	21
16 IV	02:47	142	131	0.56	22	.01	0	21
16 IV	02:57	144	198	0.55	20	.01	5	21
16 IV	03:16	148	155	0.62	22	.01	3	21

APPENDIX 1.—(concluded).

Date (1964)	Time (CET)	Lunar azimuth (deg)	Orientation azimuth (deg)	Vector length	Number of animals	Significance level	Days since collection	Lunar stage: days
16 IV	03:26	150	145	0.60	18	0.1	0	21
16 IV	04:02	158	233	0.65	11	.01	3	21
16 IV	04:17	161	141	0.47	15	.05	5	21

[a] Experimental animals (*Talitrus saltator*) were collected during daylight hours at several sites along the straight, continuous beach located about 40 km northwest of Naples. "Correct" orientation, perpendicular to that shore line, is at an azimuth of 235°. Experiments were conducted in a level open field about 1 km east of Lido di Licola. Nighttime air temperatures were between 5° C and 12° C. The observation chamber was heated in a water bath to 20 to 22° C, and a supply of $CaCl_2$ crystals, with color indicator, was within the chamber, which was about 30 cm in diameter and 5 cm deep, covered by a glass lid. Compass and clock were simultaneously photographed with the observation chamber, out of sight of the animals. All data are for second photographs, taken after the animals had been in the observation chamber for 5 min. Statistical significance evaluated by figure 15 of ref. 7; probability levels are not exact because of interactions between animals. Between collection and observation, the animals were stored at room temperatures in light-tight containers, including a strip of paper towel moistened with seawater.

APPENDIX 2

Malibu Experiments[a]

Date (1963)	Time (PST)	Lunar azimuth (deg)	Orientation azimuth (deg)	Vector length	Number of animals	Significance level	Days since collection	Lunar stage: days
20 VII	21:28	184	205	0.73	20	.01	0	10
20 VII	21:36	187	204	0.55	18	.01	0	10
20 VII	21:53	191	201	0.74	21	.01	0	10
20 VII	22:08	195	185	0.54	25	.01	0	10
20 VII	22:18	198	166	0.58	23	.01	0	10
20 VII	22:30	201	183	0.65	29	.01	0	10
20 VII	22:46	205	189	0.80	20	.01	0	10
20 VII	22:58	208	178	0.59	20	.01	0	10
20 VII	23:14	211	174	0.46	26	.01	0	10
20 VII	23:25	214	179	0.61	24	.01	0	10
20 VII	23:36	216	185	0.89	27	.01	0	10
20 VII	23:45	218	166	0.48	27	.01	0	10
20 VII	23:55	220	194	0.52	27	.01	0	10
21 VII	00:18	225	167	0.60	11	.05	0	10
21 VII	00:28	227	184	0.68	23	.01	0	10
21 VII	00:38	229	215	0.66	12	.01	0	10
21 VII	00:48	231	120	0.56	23	.01	0	10
21 VII	00:57	232	159	0.68	25	.01	0	10
21 VII	01:04	233	176	0.68	28	.01	0	10

APPENDIX 2.—(continued).

Date (1963)	Time (PST)	Lunar azimuth (deg)	Orientation azimuth (deg)	Vector length	Number of animals	Significance level	Days since collection	Lunar stage: days
24 VII	21:12	132	178	0.62	36	.01	0	14
24 VII	21:20	135	191	0.58	24	.01	0	14
24 VII	21:28	137	152	0.72	21	.01	4	14
24 VII	22:06	14[illegible]	206	0.48	21	.01	0	14
24 VII	22:20	147	194	0.55	20	.01	0	14
24 VII	22:48	154	183	0.77	21	.01	0	14
24 VII	23:06	158	165	0.63	13	.01	0	14
24 VII	23:30	164	181	0.79	20	.01	4	14
24 VII	23:37	166	185	0.57	20	.01	0	14
24 VII	23:45	168	177	0.75	17	.01	0	14
25 VII	00:03	173	188	0.43	20	.05	0	14
25 VII	00:10	175	179	0.64	22	.01	0	14
25 VII	00:23	179	166	0.82	11	.01	4	14
25 VII	00:33	182	163	0.40	19	.05	0	14
25 VII	00:45	186	204	0.48	24	.01	0	14
25 VII	01:00	190	192	0.78	10	.01	0	14
25 VII	01:14	194	181	0.94	9	.01	4	14
25 VII	01:50	202	151	0.78	13	.01	0	14
25 VII	01:58	204	163	0.45	22	.01	0	14
25 VII	02:09	207	137	0.66	13	.01	0	14
25 VII	02:23	210	221	0.59	13	.05	4	14
25 VII	02:35	213	133	0.47	22	.01	0	14
25 VII	03:01	218	158	0.72	28	.01	0	14
25 VII	03:18	222	182	0.83	26	.01	0	14
17 X	18:53	137	206	0.59	23	.01	3	10
17 X	19:48	152	190	0.46	31	.01	2	10
17 X	20:06	157	180	0.67	26	.01	2	10
17 X	20:16	160	157	0.61	2	.01	3	10
17 X	20:26	163	163	0.63	19	.01	2	10
17 X	20:40	167	187	0.67	21	.01	3	10
17 X	20:55	172	201	0.68	19	.01	2	10
17 X	21.08	176	132	0.62	18	.01	3	10
17 X	21:21	180	159	0.67	26	.01	2	10
17 X	21:40	186	157	0.90	24	.01	3	10
17 X	21:53	191	180	0.75	20	.01	2	10
17 X	22:10	196	150	0.53	23	.01	2	10
17 X	22:22	200	164	0.78	25	.01	3	10
17 X	22 36	204	154	0.7	13	.01	2	10
17 X	22:56	210	184	0.70	22	.01	3	10
17 X	23:06	213	167	0.89	27	.01	2	10
17 X	23:36	221	166	0.70	18	.01	3	10
17 X	23:48	223	175	0.91	21	.01	2	10
18 X	00:00	226	152	0.52	12	.05	3	10
18 X	00:08	228	184	0.54	13	.05	2	10
18 X	00:20	231	199	0.77	20	.01	2	10

APPENDIX 2.—(concluded).

Date (1963)	Time (PST)	Lunar azimuth (deg)	Orientation azimuth (deg)	Vector length	Number of animals	Significance level	Days since collection	Lunar stage: days
18 X	00:36	234	180	0.40	26	.05	3	10
18 X	00:51	237	178	0.35	30	.05	2	10
18 X	01:07	240	229	0.58	21	.01	3	10
18 X	01 18	242	209	0.61	[illegible]	.01	2	10
18 X	02:00	248	190	0.46	22	.01	2	10

[a] Experimental animals (*Orchestoidea corniculata*) were collected during daylight hours from east end of beach fronting on "The Colony" in Malibu, California. Correct orientation, perpendicular to that shoreline, is at an azimuth of 193°. Experiments were conducted atop the Biology Building at California State College, at Northridge, California. Nighttime air temperatures ranged from about 12° C to 18° C. For other experimental details, see footnote to Appendix 1.

APPENDIX 3

Published Records of Non-significant[a] Moon Orientation by Talitrids

PAPI AND PARDI; ref. 3:
Table 3, observations 3, 4, 6, 7, and 12
PARDI AND ERCOLINI; ref. 6:
Table 1a, observations 1, 2, 3, 4, 6, 7, and 12
Table 1b, observations 4, 5, 14, and 17
Table 2a, observations 2, 3, 4, and 5
Table 2b, observations 1 and 2
Table 3a, observations 4 and 5
Table 3b, observations 4, 5, 6, 7, and 8

[a] Vector length not different, at 0.05 level (see footnote 3 in text) from random scatter on the basis of numbers of animals used. Number of animals determined by dividing number of record positions by number of photographs or counts.

APPENDIX 4

Visual Observations of Orientation Which Apparently Are Duplicate Measurements of the Same Animals Previously Photographed

PARDI AND ERCOLINI; ref. 6:
Table 1a, observations 5, 7, 9, 11, 13, and 15
Table 1b, observations 5, 7, 9, 11, 13, 15, 17, and 19

DISCUSSION

LINDAUER: Have you more information concerning the experience of animals prior to testing? How long has an animal to see or to learn the Moon movement across the sky until he is familiar with this?

ENRIGHT: One aspect of this hypothesis, which does make it testable, is the proposition that if animals are kept under constant conditions in the laboratory for a period of two weeks or longer, then they should show only the constant-angle orientation, and show no evidence for time compensation in the orientation, as contrasted with freshly collected animals. This is consistent with the few data which are available. It is also true, however, that animals that have been kept in the laboratory for a longer period of time are less likely to show any consistent choice of direction and one must distinguish between these two.

SHOOP: Do you have any data on individual behavior as related to group behavior? Do individuals respond as groups do? Are these all group data that you presented?

ENRIGHT: These are all group data. My own qualitative impression is that the animals do not influence each other's choice of direction very much even though they crawl over and bump into each other occasionally.

GRIFFIN: Is it true that the animals oriented in the opposite way under water?

ENRIGHT: Yes, but there was no claim for this with regard to the Moon compass orientation. The reverse orientation was claimed only for Sun orientation, and I have been unable to reproduce this observation. Animals actually swimming in sea water seem to orient in the same direction as those in a dry chamber. There is an additional complication. It is now claimed in the literature that talitrids orient in the same direction as they do in a dry chamber, if you put them in fresh water; it is only in salt water that they orient away from the beach.

WALCOTT: What would be the consequence in the orientation if your animals were using a time clock based on the Sun rather than on the Moon?

ENRIGHT: It would vary from night to night, and hour to hour.

BULLOCK: Curt Richter cites many cases of rhythm in humans which are only manifested after some kind of clinical experience that he regards as a shock. In other words, he supposes that the endogenous clock is there, but it is not a single clock. It is a lot of independently phased cells, which are individually going along at the normal rate, but out of step with each other. Some special environmental trigger, which he calls clinical shock in the human patients, brings all these cells into synchronization so that they can take control of the organism and the rhythm then becomes manifest in overt signs.

ENRIGHT: I have difficulty imagining what the environmental trigger could be.

BULLOCK: Might it be moonrise or is it the time the animal emerges from the sand?

ENRIGHT: I have a hard time imagining how Moon synchronization of this kind of a clock would work, even though I have proposed the hypothesis.

BULLOCK: Put it the other way around. It is the cold or the fog that lets the cells, the numerous endogenous clocks that have the same intrinsic rhythm, drift apart. When the animal can see the environmental sign, all his endogenous clocks get into synchrony, so that they, in your words, take control.

WATERMAN: Why do you assume that the Moon rather than the tides synchronizes this rhythm?

ENRIGHT: On the Pacific coast the tidal factors could represent a very good synchronizing agent for some sort of a lunar rhythmicity. The best argument against this, however, is that tides in the Mediterranean area are of very small amplitude and the animals live so far up the beach that direct experience of the tides seems unlikely.

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SESSION V

Sensory Mechanisms—Electrical and Magnetic Cues

Chairman, FRANK A. BROWN

Magnetic Effect on Dancing Bees

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THE BIOLOGIST may be aware of the fact that for billions of years the Earth's magnetic field has offered two important orientation cues to living organisms: (1) compass directions may be derived from it and (2) periodic 24-hour oscillations offer a geophysical time signal that contains constant parameters independent of daylight and temperature.

In this paper we shall try to bring evidence that bees are actually sensitive to the Earth's magnetic field. The sensitivity range will be dealt with and, finally, the question will be posed as to whether magnetoreception is used for orientation by the bees.

DISTURBANCE OF GRAVITY ORIENTATION BY MAGNETIC FIELD

After their return to the hive, successful forager bees inform by the wagging dance other hive mates where food can be found. In this context only the indication of the direction toward the goal is of interest; the angle between the food source and the Sun is transposed with respect to gravity (ref. 1). When comparing the records of more than ½ million dances, it becomes evident that the direction of the wagging line contains regular deviations that follow a typical diurnal pattern (fig. 1A). This daily pattern, in principal, can be reproduced if the azimuth of the goal and the specific geophysical factors (s.b.) remain constant.

However, the misdirection (Missweisung) completely changes when the comb, together with the dancing bees, is turned by 90°, e.g., from an east-west position to a north-south position (fig. 1B). Since the stimulus from the gravity field remained unchanged, we presumed that the Earth's magnetic field may have affected the dancing bees in a different way: In the east-west position the wagging line of the dance can be affected only by the vertical vector of the Earth's magnetic field; in the north-south position by the vertical and the horizontal vector.

The Missweisung completely disappears when the magnetic field is compensated (fig. 2). The dancers now orient exclusively with respect to gravity.

SENSITIVITY RANGE AND ADAPTATION

When analyzing the diurnal curves of the "Missweisung" in more detail, the following correlations become evident:

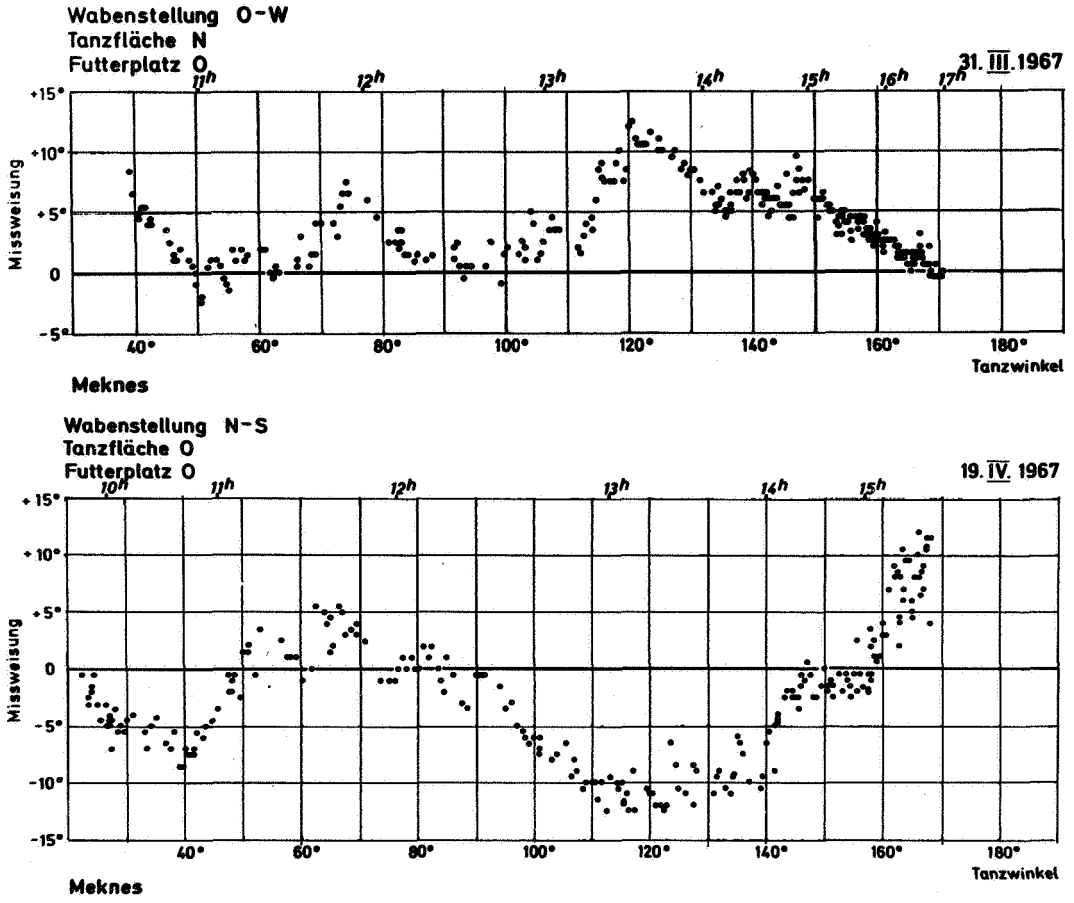

FIGURE 1. Dancing bees had visited a food source 400 m eastward of the hive. In the wagging dance they transpose the angle between Sun and goal into the gravity field. This angle has to be changed all day long corresponding with the Sun's movement (abscissa). Each spot indicates average of 10 records in one dance, whereby only spots on the zero line correspond to dances without mistake. Deviations are not randomly scattered above and below zero line but follow a diurnal curve depending on position of the dance floor in the Earth's magnetic field. (A) Hive position east-west; dance floor facing northwards. (B) Hive position north-south; dance floor facing eastwards.

(1) The curves pass through zero when the wagging line corresponds to the plane of inclination. Thus the position of the dancing area must be taken into consideration. In the first position the comb is directed north-south with the dancing area on the east side; zero points are found at 25° and 205° (fig. 3). In the second position the dancing area is on the west side and the zero points at 155° and 335° (fig. 4). In the third and forth position, the beehive is directed toward the east-west. In this case the dancing area (south or north) is always vertical to the plane of inclination with the zero points at 180° and 360°

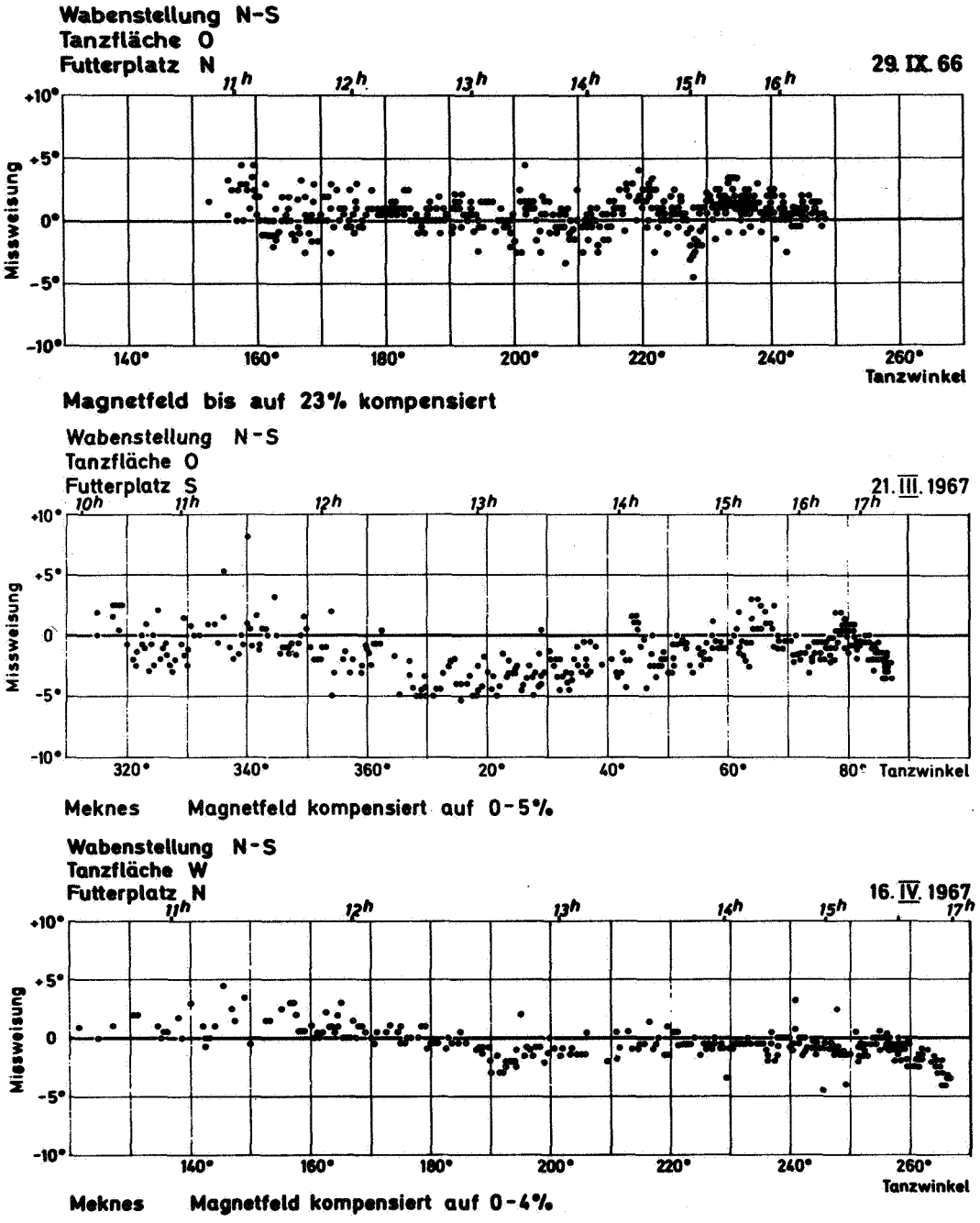

FIGURE 2. A dance floor was put in center of a Helmholtz-coil and the Earth's magnetic field was compensated up to <23 percent, <5 percent and <4 percent respectively. Diurnal curve of the "Missweisung" is flattened; dancing bees now transpose the angle between goal and Sun exclusively with respect to gravity.

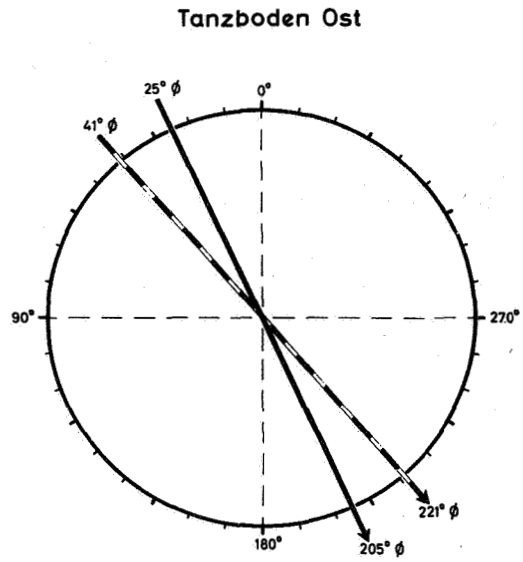

FIGURE 3. Beehive is in north-south position; dancing area ("Tanzboden") faces east. In this situation inclination in Frankfurt is identical with dancing angles 25° (to the left upwards) and 205° (to the right downwards) (solid arrow). In Meknes, Morocco, the inclination passes 41° and 201°. "Missweisung" disappears in this section of the gravity field.

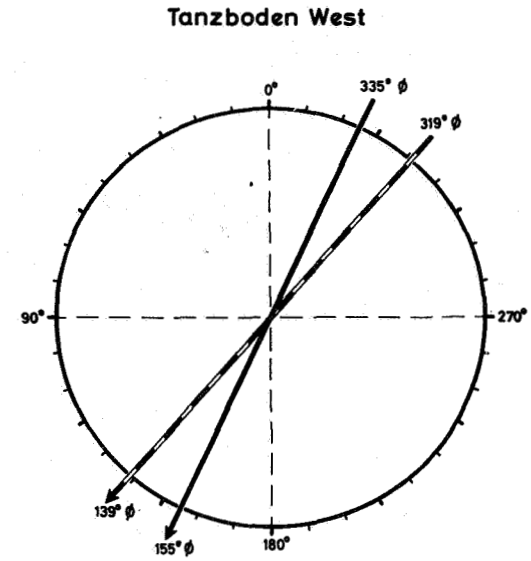

FIGURE 4. Beehive in north-south position; dancing area faces to west. "Missweisung" disappears at 335° and 155° (Frankfurt), or 319° and 139° (Meknes).

corresponding to the vertical component on the northern as well as on the southern side of the comb. Of all 62 diurnal curves of the "Missweisung" available to date, only one does not fit with our theory. On that day a gale of wind had partly removed the double cover of the tent and had caused an uncontrolled disturbing influence of incident light.

The daily curves of the "Missweisung" obtained in Morocco in 1967 were also checked with respect to the rules observed. Owing to the inclination of 49°, the zero points were now 41° (221°, respectively) on the eastern side and 139° (319°, respectively) on the western side of the comb. All curves from Morocco were in full accord with our expectations. Furthermore, we can state that the daily curves only deviate by 0.2° from the expected values, taking into account all dance angles from 2° before, to 2° after, the calculated zero points (standard deviation $\sigma = \pm 3.7°$). We concluded that bees, dancing parallel to the direction of the magnetic field lines, orient themselves without error and exclusively in respect to gravity.

(2) In all other directions, the influence of the magnetic field may be described by the following function (fig. 5):

$$Mi = \log (\sin \alpha \therefore \Delta\gamma)$$

α = direction of the wagging line with respect to the gravity field

$\gamma = 10^{-5}$ oersted

$\Delta\gamma$ = variations of the magnetic field in time units

This rule applies to the north-south comb directions. Experiments with the combs oriented east-west are now being carried out.

The data given, so far, show that bees are sensitive to variations of the magnetic field in the range from 0 to 300 γ. However, only dynamic changes are of importance. When a static artificial magnetic field is produced (3 to 10 times stronger then the Earth's magnetic field), only the dispersion of the "Missweisung" becomes higher.

Furthermore, error free dances only begin 30 to 45 min after the magnetic field is artificially compensated (fig. 6). On the other hand, when the magnetic field whether natural or artificial changes rapidly (by more than 1 $\gamma/1°$ of azimuth of the Sun's path) the bee reacts to this rapid rise or fall with only about one tenth of the normally observed "Missweisung." We thus have a process of adaptation that appears to be like hysteresis or magnetic lag effects.

COMPETING GRAVITY AND MAGNETIC FIELDS

By tilting the comb as far as the horizontal, the orienting force of gravity can be continously diminished. The effect of the magnetic field now becomes more apparent. The dancing bees become more and more confused. The dispersion in indicating the grav-

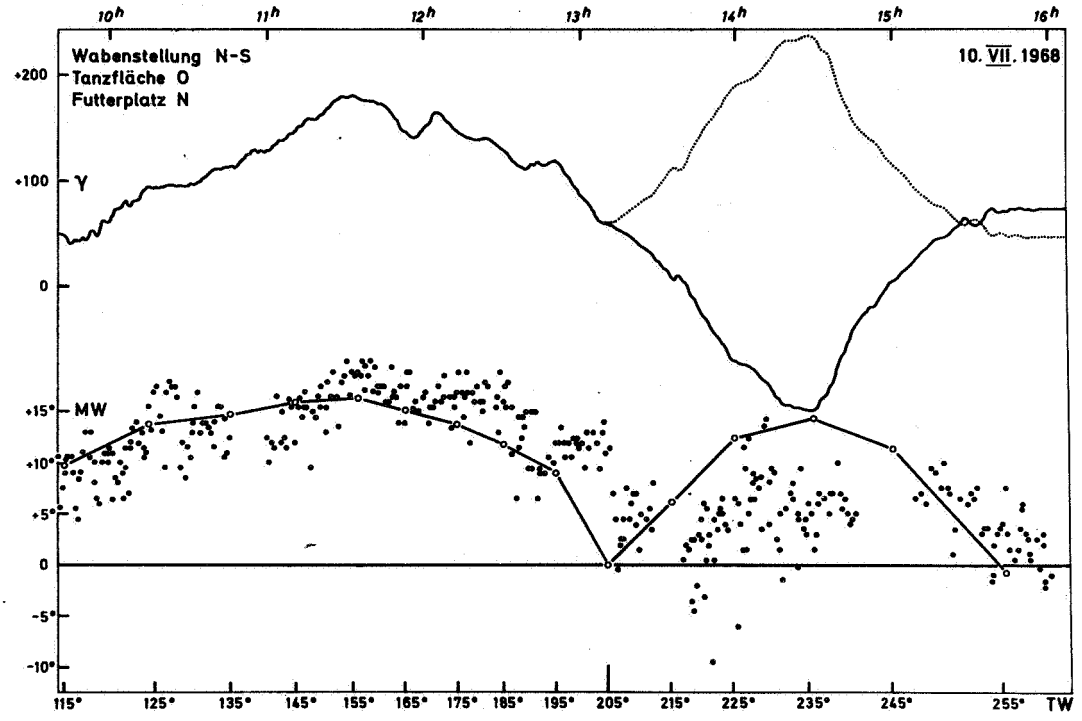

FIGURE 5. Diurnal curve of "Missweisung" follows the function: $Mi = \log (\sin \alpha \cdot \Delta\gamma)$. Curve above is magnetic variation measured during the records of the dances. Curve below is calculated from function above. Curve of the "Missweisung" function fits well into this function. *MW* = "Missweisung."

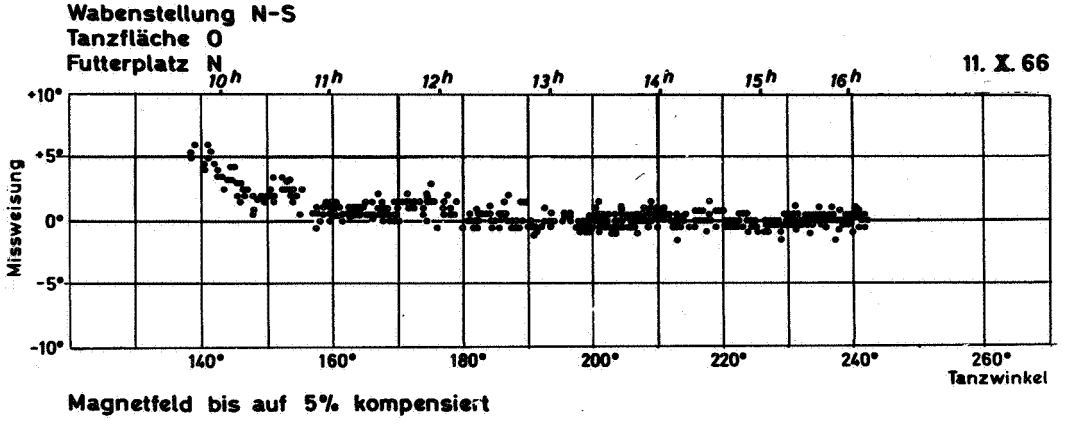

FIGURE 6. In this experiment dances were recorded immediately after magnetic field was compensated. There is a time for adaptation of about 45 min.

ity angles rapidly increases and the bees tend to "cling" to the horizontal components of the magnetic field or to the plane of inclination depending on whether the hive is directed north-south, east-west, northeast-southwest, etc.

If the bees are totally deprived of the possibility to orient themselves with respect to gravity by laying the comb flat, the dancers are at first disoriented. If the hive is left in this position for about 3 weeks, orientated dances are observed in increasing number pointing preferably in a north-south or east-west direction (fig. 7). When the magnetic field was then compensated, the dances again were disorientated; when increased three times the Earth's magnetic field, the north-south and east-west directions were even more preferred (figs. 8 and 9).

ORIENTATION IN THE MAGNETIC FIELD

The results reported to date seem to indicate that the Earth's magnetic field is only disturbing the orientation of the bees. M. Oehmke, our student, has found a situation in bees revealing true orientation to the Earth's magnetic field. When a swarm of bees is encased in an empty cylindrical box with a central entrance in the bottom, the bees start sticking small lumps of wax all over the box lid. Finally the building bees, 600 to 1000 or even more, all start building one, two, or three pieces of comb in a defined direction (fig. 10). In the first series of experiments, eight colonies were used of known origin which had, for generations, built their combs in a north-south direction. Daughter swarms were taken from these colonies and permitted to build their combs in the round boxes. All these colonies, without exception, built their combs in the same direction as they had done in the hives from which they originated (standard deviation $S_{\bar{x}} = \pm 2°$) (fig. 11). Neither gravity nor incident light could have given any orientation clues. If the declination of the magnetic field is changed artificially, the direction of the combs is changed in the same sense. We consider the magnetic field as a potential parameter by which the bees could orientate under these circumstances.

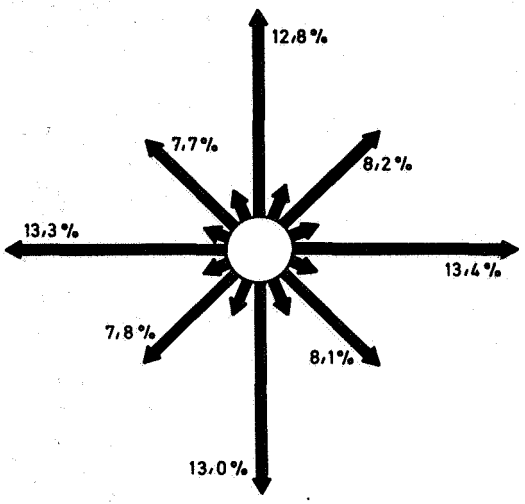

FIGURE 7. When dancing area is in a horizontal position, dances at first are completely disoriented. After 3 weeks, however, a preference was given to N-, S-, E-, W-direction.

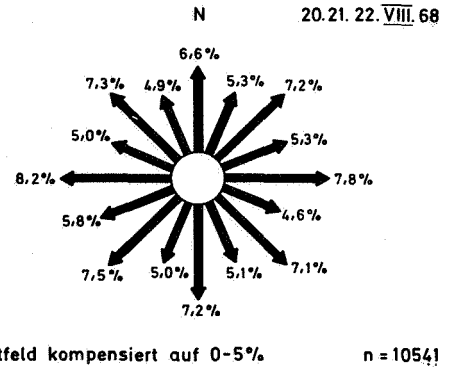

FIGURE 8. In compensated magnetic field, dances remained disoriented in this horizontal position.

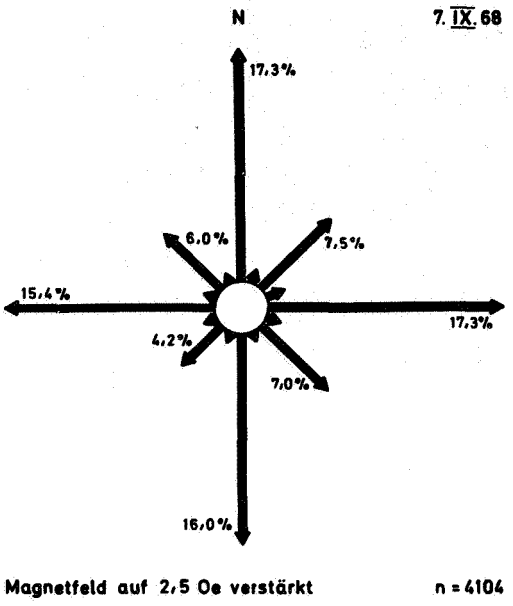

FIGURE 9. In increased magnetic field, main points of compass are still more accentuated.

MECHANISM OF PERCEPTION

The actual mechanism is still not known; it seems improbable that there are any specific receptors. In theory electric induction in the sense organs or in the nerve fibers might be considered as well as paramagnetic effects in the sense organs (e.g., the gravity receptors) or protein molecules acting as dipoles during the wagging dance on which the magnetic force of the magnetic field could act in a specific way. The mechanisms based on paramagnetic effects seem more probable with respect to the phenomenon of adaptation. We hope to test, by experimental analysis, whether this hypothesis is valid.

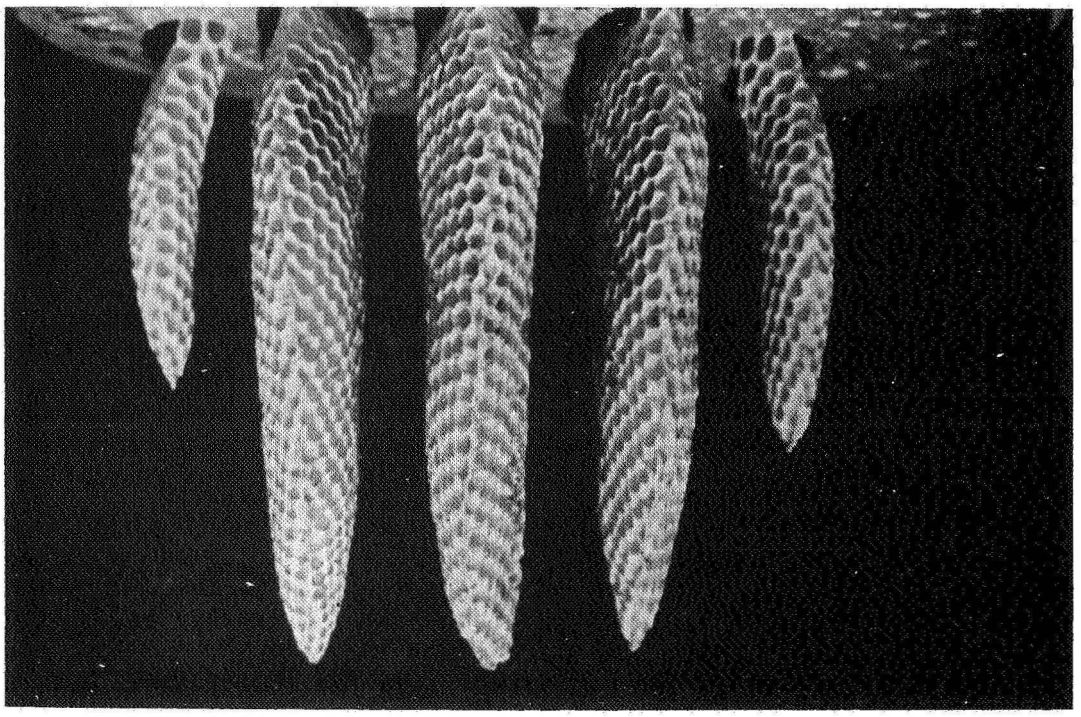

FIGURE 10. Thousands of building bees unanimously start their combs oriented in the same direction.

DISCUSSION

ENRIGHT: How are your angles measured? Is it simply a visual estimate?

LINDAUER: We use special equipment: a rectangular plexiglass sheet in which there is a second rotatable plexiglass circular sheet with white parallel lines engraved on it. These lines are adjusted along the wagging lines of the dancing bee.

The accuracy of the measurement amounts to less than ±0.5 degree. However, the following precautions must be taken: (1) The bees must be in a good dancing mood so that they will not interrupt the wagging lines. To ensure this, there must be high quality food available and no competition from other crops in the open field. (2) The feeding table should be more than 400 m away since dancers indicating close goals (less than 300 m) perform wagging lines of slightly divergent angles, which decrease to 0 as the table is moved to 400 or more meters. (3) To ensure exact data, 10 measurements in one individual dance are taken; therefore, each point on the curve indicates 10 records from one single dancing bee.

ENRIGHT: Were the bees single identified individuals?

LINDAUER: For statistical purposes, care is taken to select, by chance, individual bees arriving at the dancing area from the feeding table. A group of 20 to 30 marked bees is kept at the feeding table. This group changes, in part, from day to day.

ENRIGHT: How did you get recruits, when the foragers were dancing in the horizontal position, to tell each other where the food was?

LINDAUER: Since dancers in a horizontal position are disoriented and never indicate the direction toward the food, recruited novices search around the hive randomly. Subsequently very few recruits come to the feeding table.

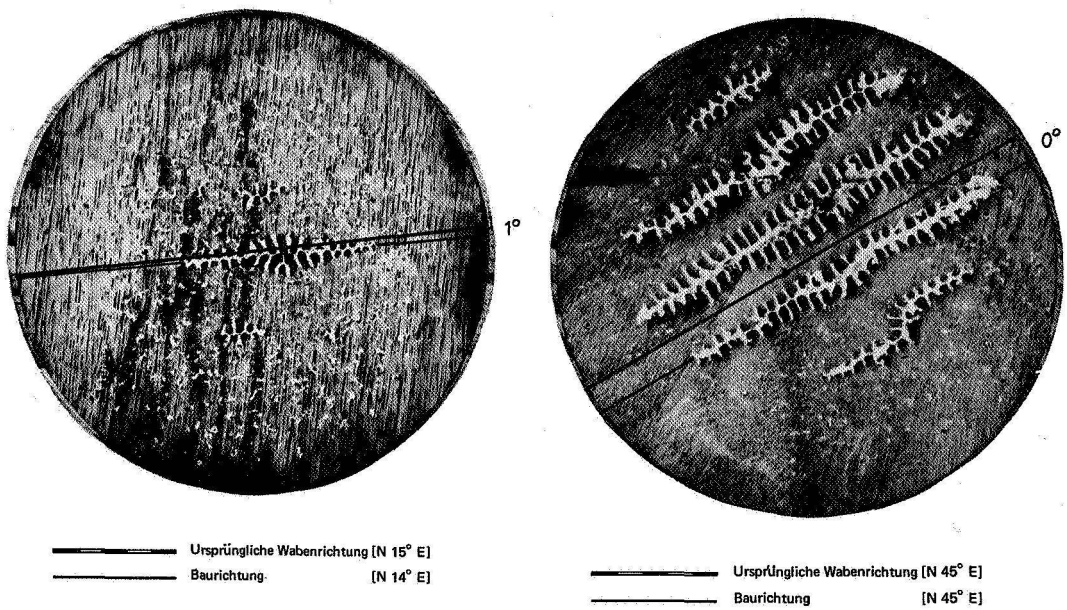

FIGURE 11. Swarm encased in cylindrical box builds new combs in same compass direction as there was in the mother hive. Top: deviation 1°; bottom: deviation 0°.

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The Influence of Magnetic Total Intensity and Inclination on Directions Preferred by Migrating European Robins

(Erithacus rubecula)

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IN THEIR FIRST MIGRATORY PERIOD a simple directional orientation would lead migrating birds to an area appropriate for wintering. The relocation of a specific area, or homing after displacement, however, may need more complex orientation capacities (bicoordinate orientation or true navigation). In this paper I will discuss only directional orientation, which I will call "migratory orientation."

The possibility that birds use the Earth's magnetic field for orientation has often been discussed. Yet the older hypotheses which discussed the role of magnetic cues in bird orientation mostly pertained not to migratory birds, but to homing pigeons (refs. 1 to 4). All these hypotheses were rather speculative and were based upon little or no experimental material. Experiments that tried to influence the directional preference of captive birds by means of artificial magnetic fields lacked conclusive results (refs. 5 and 6), yet the intensity of these artificial magnetic fields is unknown.

Merkel and Wiltschko (ref. 7) and Wiltschko (ref. 8) showed that the directing cues for migrating European robins are provided by the Earth's magnetic field. Experiments by Southern (ref. 9) showed that the orientation of ring-billed gull chicks is influenced by magnetic disturbances. Experiments using conditioning of the cardic rhythm show that birds (pigeons) are sensitive to magnetic fields of the same intensity as the Earth's field (ref. 10). An influence of magnetic fields on the orientation behavior of some invertebrate species was described during recent years by Schneider (ref. 11), Becker (ref. 12), and Lindauer and Martin (ref. 13) for insects, and by Brown (ref. 14) for planarians and snails.

In this paper I will try to analyze some magnetic cues which enable birds to select their migratory direction.

MATERIALS AND METHODS

The methods used in my recent experiments were the same as those described in detail in an earlier publication (ref. 8). The orientation cage, made of wood and plastic, was octagonal, 1 m in diameter and 35 cm

high. It contained eight radially positioned perches which were connected to microswitches that produced a signal for every hop of the bird. These data were punched into a paper tape, which was later processed by computer. I used this automatic method of data gathering so as to avoid subjective mistakes in interpretation.

The Earth's magnetic field in Frankfurt is 0.46 G, magnetic north at 360° = geographic north, and +66° inclination. The different magnetic fields used during this study were produced by screening off parts of the Earth's magnetic field by a steel vault and by using Helmholtz coils (2-m diameter and 1-m clearance). The inhomogeneity in such a magnetic field is less than 4 percent in and around the cage. Tests were conducted at field intensities ranging from 0.16 G to 1.05 G in different directions and with inclinations between +66° and +8° and at −66°.

The tests were made in five different places in the Zoologic Institute and the Botanic Garden. During the experiments the test cage was illuminated by a dim, indirect light with an intensity of 0.03 lux, for we found that in complete darkness the birds slept and did not show any restlessness. My test bird is the European robin *(Erithacus rubecula)*, a species that can be found in all parts of Europe except in Northern Scandinavia. This species migrates to the Mediterranean and North African countries. I tested more than 200 birds altogether, each test being carried out with only one bird at a time — in one cage where he stayed the whole night.

The mean directions of each night (calculated by computer) are comprised in the mean direction α_m and the concentration a_m of a series. The a_m is tested by the Rayleigh test for directional preference, and differ-

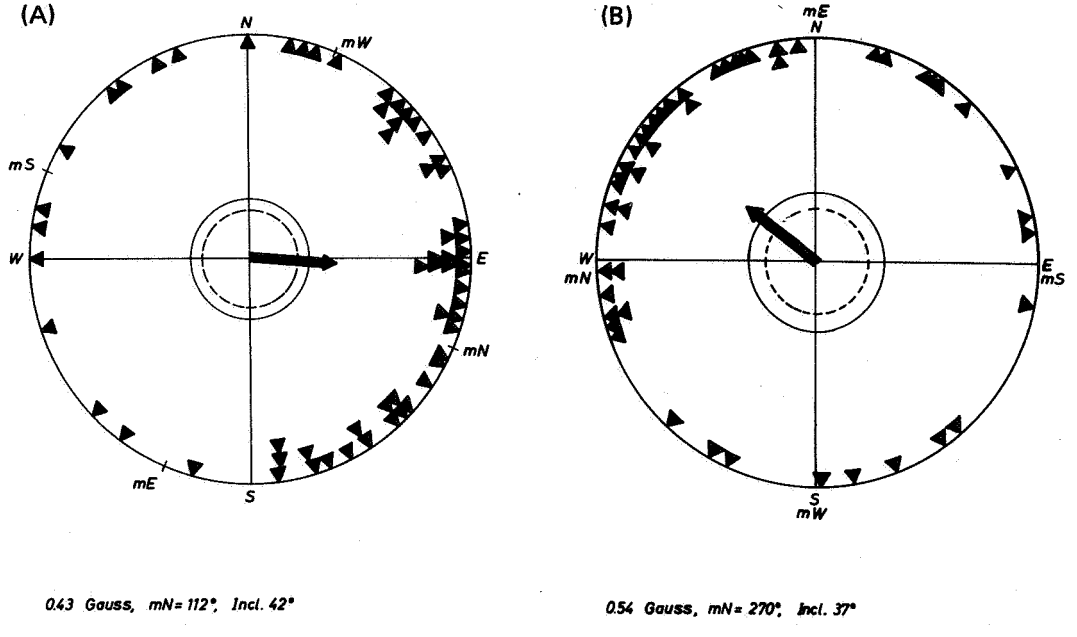

FIGURE 1. Mean directions in spring, magnetic north turned (A) to the ESE and (B) to the W.

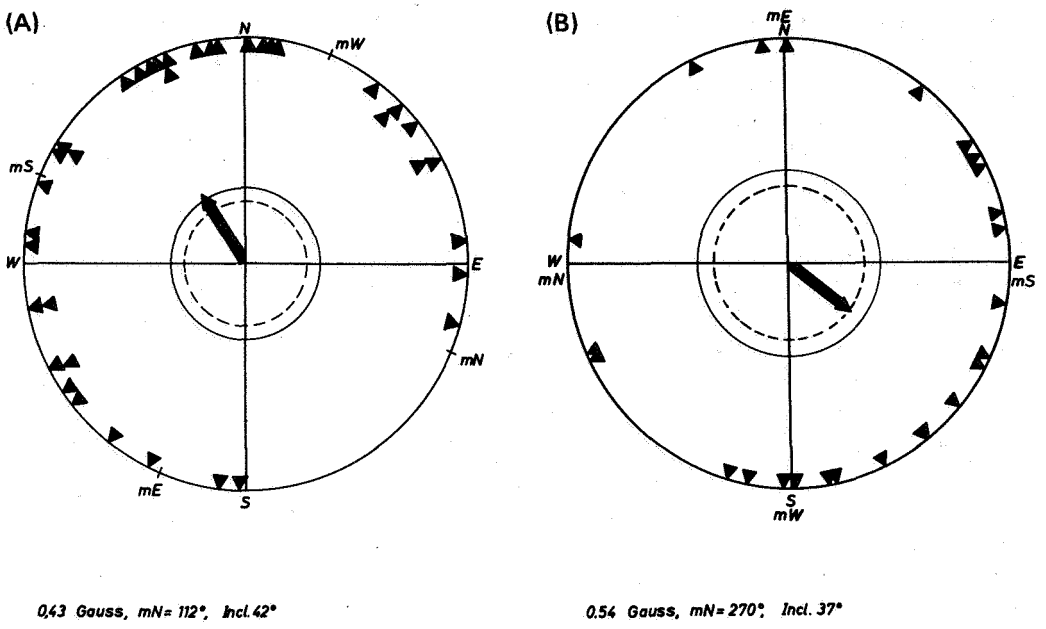

FIGURE 2. Mean direction in autumn, magnetic north turned (A) to the ESE and (B) to the W.

ences in mean directions of different series are tested with Watson and William's test and/or chi² test (ref. 15). In this paper's illustrations, the mean direction of single nights are represented by triangles and a circle and the mean direction α_m of the test series is shown as a vector originating from the center. The length of this vector represents the concentration a_m, and the two inner circles are the 5-percent (dotted) and the 1-percent significance border of the Rayleigh test. If the experimental north direction differs from geographic north, it is stated below the diagram and is marked as "mN" on the circle (0° = 360° = geogr. N; 90° = geogr. E; 180° = geogr. S; and 270° = geogr. W).

RESULTS

In order to show that robins use information they derive from the magnetic field for migratory orientation, I will refer to data from former experiments where I changed the direction of the magnetic field and tried to maintain approximately the normal field intensity (ref. 8).

The migratory direction of robins in spring lies between NW and NE. When the north direction of the experimental magnetic field was turned to ESE (0.43 G, mN = 105°, I = 42°) the robins showed a mean direction of 92° during springtime (fig. 1A), which is experimental NNW ($p < 0.01$). Turning experimental north to the west (0.54 G, mN = 270°, I = 37°), I found the mean direction at 309° (fig. 1B), which is experimental NE ($p<0.01$).

In corresponding experiments in the fall the mean direction was 328°, which is experimental SSW (fig. 2A) when magnetic north was in ESE (mN = 105°) ($p < 0.01$); and at 128°, which is experimental SW (fig.

2B) when magnetic north was in W (mN = 270°) ($0.05 > p > 0.01$).

In all four cases the birds selected their migratory direction according to the direction of the magnetic field and the season.

It should be emphasized that tests with experimental north in ESE and in W were carried out in an orientation cage which was held in the same position for each individual bird. Only the direction (and to some degree the intensity) of the magnetic field was changed so that the bird could not rely on cues given by the cage itself or by the external environment.

In recent experiments we tried to narrow the limits of magnetic intensity in which the birds are able to select their migratory direction. In the next test the magnetic field intensity was reduced by about 25 percent, experimental north was in geographic north (0.34 G, mN = 360°, I = 57°). As a control we had a magnetic field of the Earth's field intensity (0.46 G, mN = 360°, I = 48°) at the same time in the same room. In the test situation I could not find any directional preference (fig. 3A), whereas the control birds showed a migratory directional preference of 42° = NE ($p < 0.01$) (fig. 3B). Former tests also showed no directional preference at 0.34 G (see table 1 and ref. 8).

In the next test series the field intensity was increased to about 150 percent of the Earth's magnetic field, experimental north remained coincident with geographic north (0.68 G, mN = 360°, I = 25°). A magnetic field of the same intensity as the Earth's magnetic field again served as the control (0.46 G, mN = 360°, I = 48°). We found that the birds lost their ability for orientation in magnetic fields of this high intensity, just as they did in fields of low intensity (fig. 4A, control 4B).

Table 1 shows a summary of all experi-

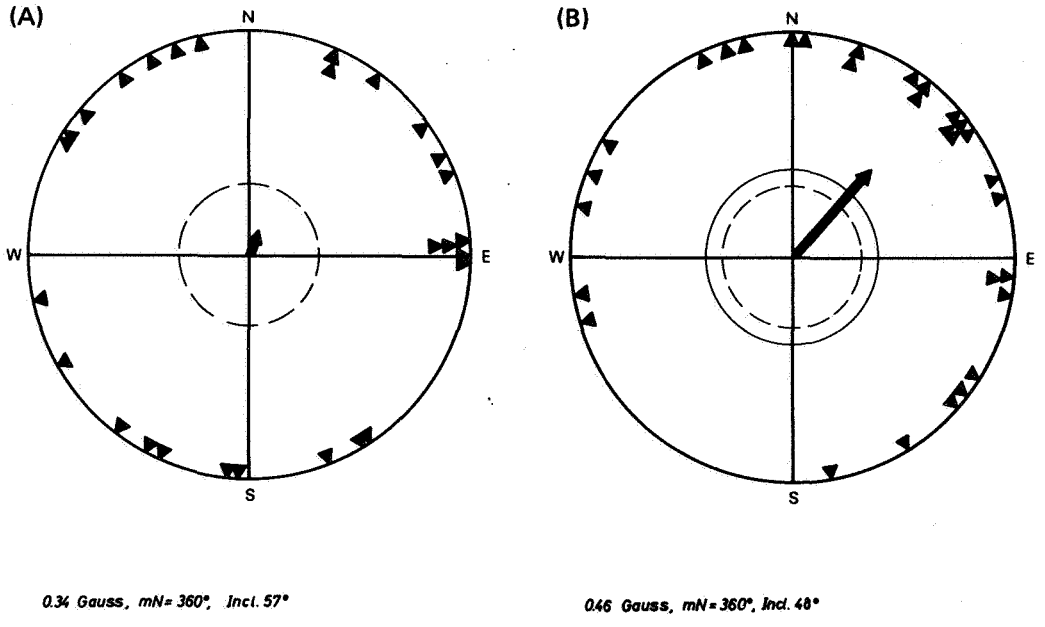

FIGURE 3. Mean directions in spring, (A) reduced field intensity and (B) normal field intensity.

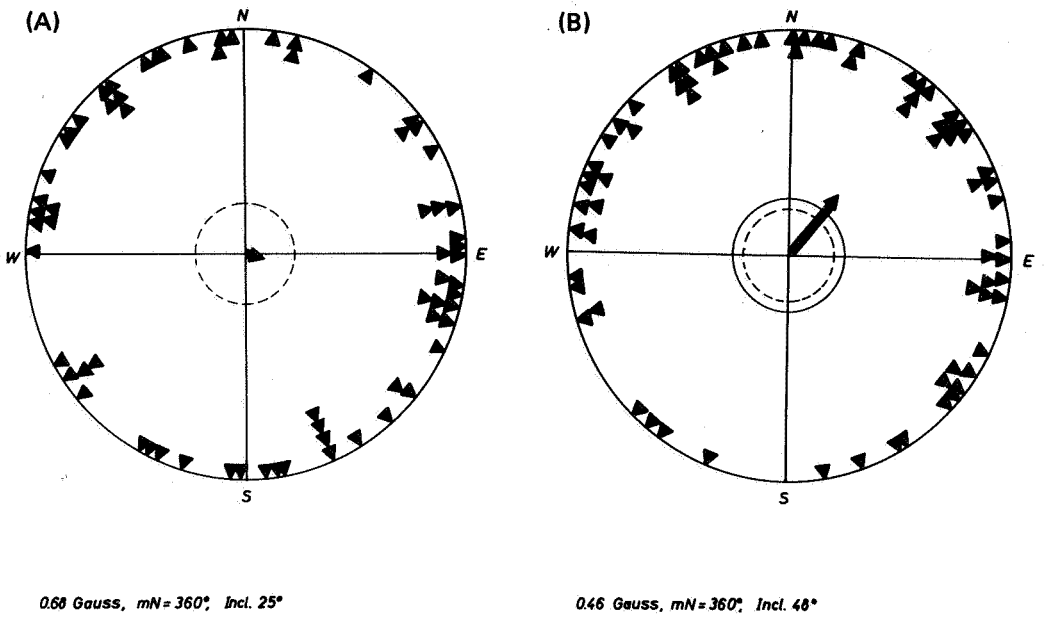

FIGURE 4. Mean directions in spring, (A) increased field intensity and (B) normal field intensity.

ments carried out in Frankfurt. The test series are classified according to the intensity of the magnetic field. This table shows that migratory orientation could be maintained only in the range between 0.34 G and 0.68 G. Further experiments will be conducted to determine whether this range is even narrower.

The range of magnetic intensity in which migratory orientation is possible is very narrow, but during fall and spring migrations the robins might come into geographic latitudes with magnetic intensities outside this range. So it is not surprising that robins, kept more than 3 days in a low field intensity of 0.16 G, again showed a directional preference for their migratory direction: test field 0.16 G, mN = 360°, I = 31°, mean direction in the fall migration period at 208°, which is SSW ($p < 0.01$) (fig. 5A). As a control, a few tests of the same birds are

TABLE 1.—*Summary of All Frankfurt Experiments*

Field intensity (G)	Inclination	Season	*n*	Significant mean direction
0.16	31°	Spring	79	.....
		Autumn	52	.....
0.34	57°	Spring	103	.....
		Autumn	74	.....
0.43	42°	Spring	62	mNNW
		Autumn	38	mSSW
0.46	66°	Spring	83	NNE
		Autumn	42	SW
0.46	48°	Spring	73	NE
0.46	12°	Autumn	18	W
0.54	37°	Spring	49	mNE
		Autumn	35	(mSW)
0.68	25°	Spring	68	.....
0.81	8°	Spring	42	.....
0.82	30°	Spring	28	.....
		Autumn	16	.....
1.05	23°	Spring	50	.....
		Autumn	32	.....

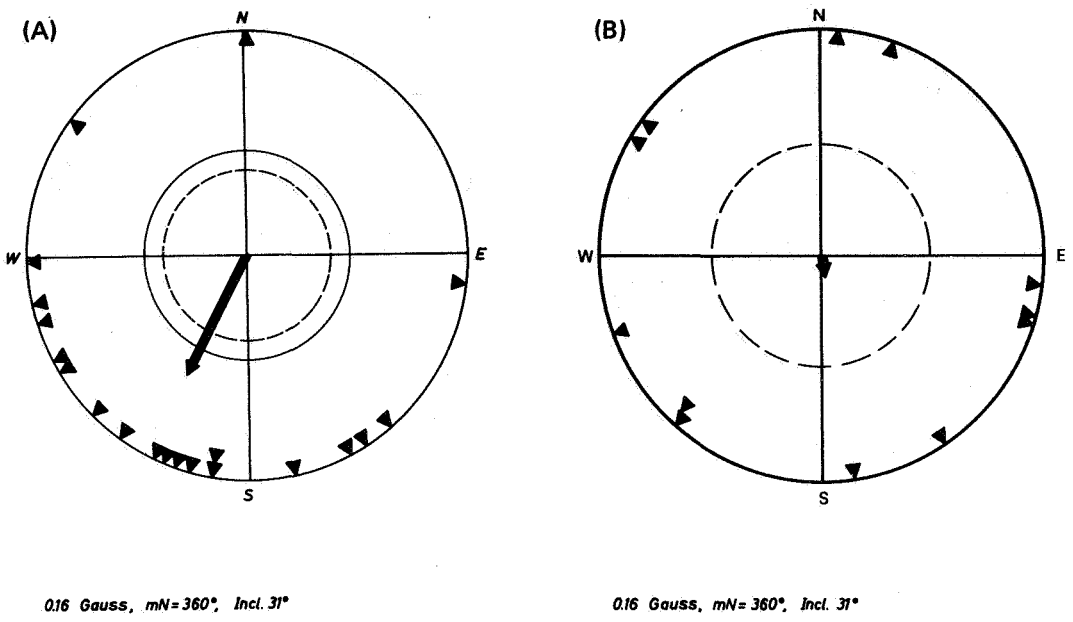

FIGURE 5. Mean directions in autumn at reduced field intensity, (A) birds accustomed to low field intensity and (B) birds housed in normal field intensities.

included when they were still kept at 0.46 G and before they were brought to live in this low field intensity (fig. 5B).

Test series that were begun in the spring of this year indicate that, after a period of becoming accustomed, migratory orientation is also possible in fields of high intensity. Birds were kept in a field of 0.81 G for at least 3 days and tested in a magnetic field of the same high intensity (0.81 G, mN = 360°, I = 8°) (fig. 6A). A directional preference of 354°, which is N, can be observed ($0.05 > p > 0.01$). Tests with birds that were not accustomed to high intensity fields served as controls (fig. 6B).

In the above described experiments the strength of the horizontal component of the magnetic field was varied greatly without influencing the birds' ability of orientation. The question now was whether the magnetic compass of the robin functions as a compass system in the horizontal plane. A magnetic field was produced in which only the inclination was changed from + 66° to — 66°, with intensity and north direction remaining the same; i.e., the horizontal component has the same strength and direction as in the Earth's magnetic field. The vertical component also has the same strength, but the opposite direction, since it is now directed upward away from the ground and toward the sky (0.46 G, mN = 360°, I = — 66°). Between the magnetic field lines and the force of gravity there is now an angle greater than 90°, whereas in the Earth's magnetic field this angle is less than 90°. The Earth's magnetic field served as a control (0.46 G, mN = 360°, I = + 66°).

The results of this test were very surprising. The same robins that had showed a mean direction of 327° in the control, i.e., NNW ($p < 0.01$) (fig. 7B), under test con-

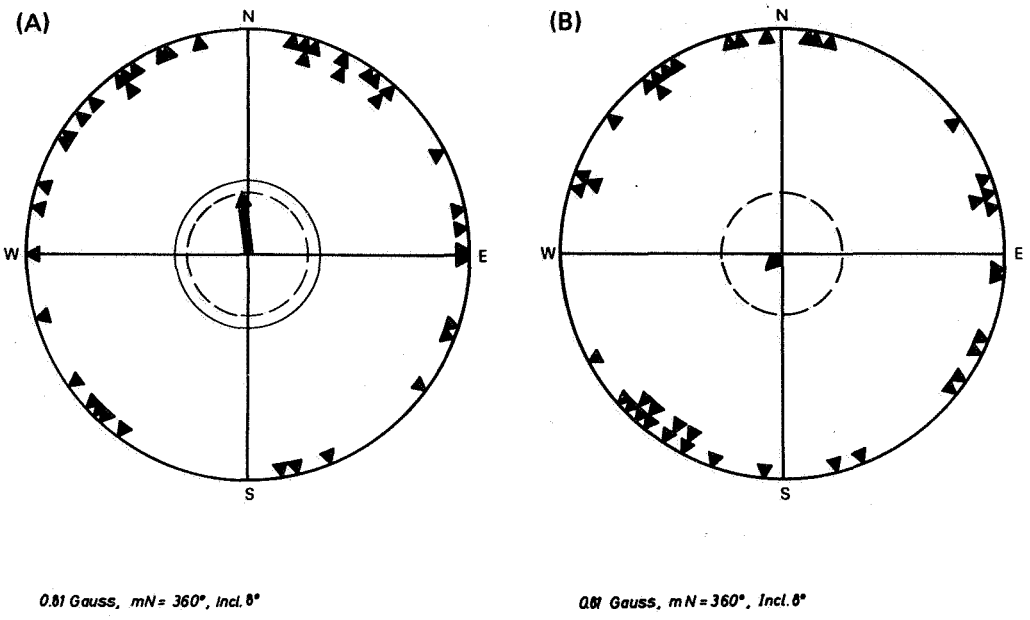

FIGURE 6. Mean directions in spring at increased field intensity, (A) birds accustomed to increased field intensity and (B) birds housed in normal field intensity.

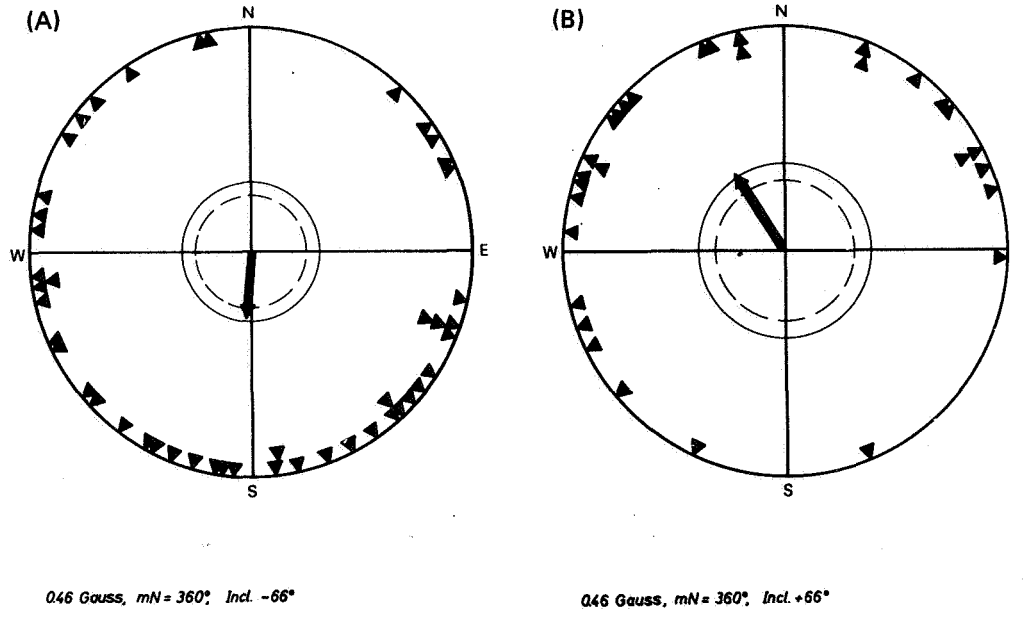

FIGURE 7. Mean directions in spring, (A) inclination negative and (B) normal Earth's magnetic field.

ditions seemed to seek their spring migratory direction in the S at 185° (fig. 7A). The Rayleigh test shows a significance of $0.05 > p > 0.01$ for the test series, yet the fact that the mean directions in test and control originated from different statistical populations is significant with $p < 0.001$.

CONCLUSION

The results show that the magnetic field provides the following cues for migratory orientation: (1) field intensity, (2) direction of the field in the horizontal plane, and (3) inclination equals direction in the vertical plane.

The intensity determines whether the field can be used as a source of information for orientation. By accustoming the birds to intensity values outside the intensity range normally encountered in migratory orientation, the intensity range can be enlarged to lower and, presumably, also to higher values. This may be important for the bird which, during migration, might come to geographic latitudes with other intensity values. The field direction in the horiontal plane provides the bird with a reference direction to orient his migratory direction.

Our tests show the following: (1) within the intensity range which enables the bird to orientate, the angle of inclination does not matter within the positive range (tests were made between $+120°$ and $+66°$); (2) variations in the inclination angle cause significant variations in the horizontal and vertical intensity components of the magnetic field. We can, therefore, assume that none of these components alone is essential for the birds' physiological perception of the magnetic field but only the resultant, total intensity, which can have any direction within the said range.

The last experiment shows the importance of the direction of the vertical component. A reversal of the vertical component causes the birds to migrate in the opposite direction. The north and the south directions in the relation system given by the direction of the horizontal component are determined by the direction of the vertical component. This means, however, that the bird cannot perceive the polarity of the magnetic field but only the axial direction of the magnetic field lines We must conclude from this that there is no compass system for the bird in the plane. The axial direction of the magnetic field without its polarity does not, however, permit a clear orientation according to the magnetic field. The bird must still use other information.

According to my present hypothesis, this additional information is provided by the force of gravity, i.e., by the knowledge of up and down. The bird can determine the angle between the gravity direction and the axial direction of the magnetic field. In the northern hemisphere this angle, γ', is in the northern semicircle always smaller than 90°. The bird looks for the biggest of all angles being smaller than 90°; this direction points to north.

Mathematically this angle γ can be expressed as follows:

$$\tan \gamma = \frac{H_h}{H_v}$$

where H_h is the horizontal component, positive in the direction of magnetic north, and H_v is the vertical component which is parallel to the force of gravity, positive in downward direction. The bird cannot perceive the direction of the components, but it can measure tan γ. The point where tan γ reaches its maximum positive value indicates to the bird the direction of magnetic north (fig. 8A). If we reverse the direction of one

of the components, the sign of tan γ becomes negative (i.e., the angle becomes greater than 90°). But the bird can find an angle with positive tan γ' on the opposite side, and he must look now for his north direction opposite to the original one (fig. 8B).

To confirm this model we are going to make the following tests: (1) reversal of both components — the birds should migrate into the same direction as in the terrestrial field; and (2) production of a field of Earth's intensity but without a vertical component — the birds should not show a clear migratory orientation.

SUMMARY

1. Field intensity determines whether the magnetic field can be used for migratory orientation.

2. The normal intensity range can be enlarged by becoming accustomed to weaker or stronger fields.

3. The birds can perceive the axial direction of the field lines but not their polarity.

4. A discussion of the hypothesis that birds can find the north direction by means of the angle between gravity and magnetic field direction was presented.

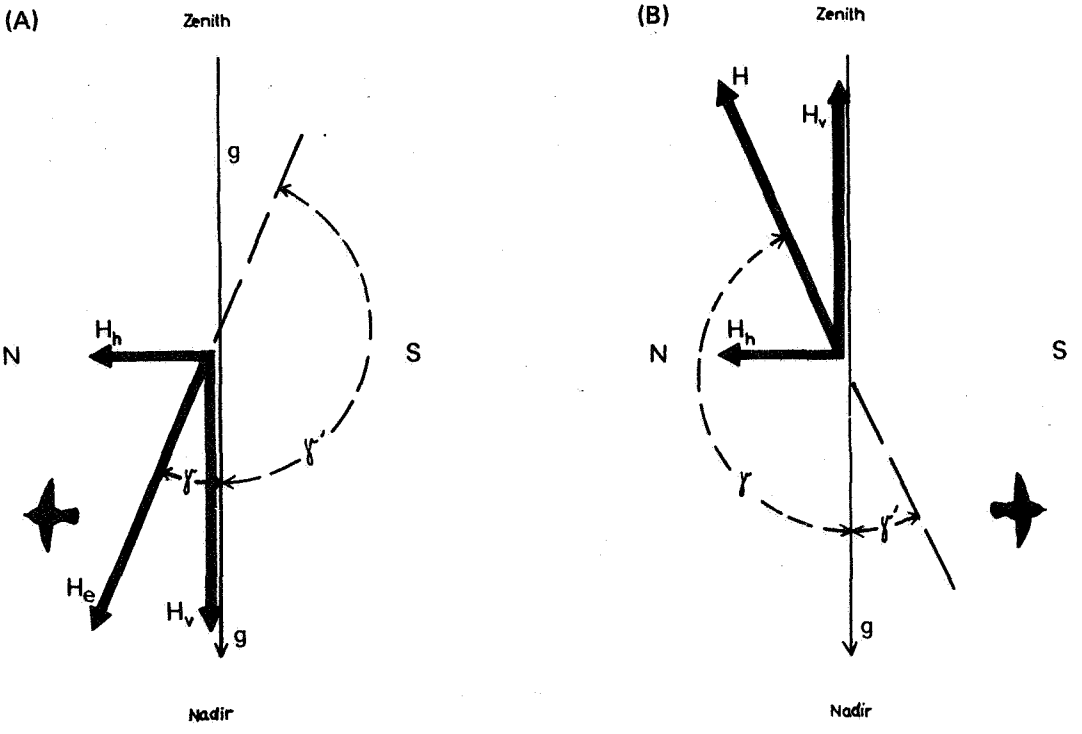

FIGURE 8. Sections through the magnetic field in a plane parallel to the force of gravity and the N-S axis; g = force of gravity; H_e = Earth's magnetic field vector; H = experimental magnetic field vector; H_h = horizontal component; H_v = vertical component; γ = angle between force of gravity and magnetic vector; γ' = supplement angle to γ. (A) Situation in the Earth's magnetic field; (B) situation when the inclination is negative.

ACKNOWLEDGMENT

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DISCUSSION

QUESTION: What was the average angular deviation for the means of the single nights?

WILTSCHKO: It was about 80° to 65°. We found high activity and directional preference in a single night are negatively correlated. Since we cannot consider the vectors for a single night, we took them all as being equal.

ENRIGHT: What percentage of the individual bird-nights would be statistically significant if you treat each observed perch-hop as statistically independent, which, of course, they are not?

WILTSCHKO: About 60 percent.

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Effects of Magnets on Pigeon Homing

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ALTHOUGH THE POSSIBILITY THAT magnetic cues might be used in avian orientation has been suggested numerous times (refs. 1 to 13), it has never gained wide support. Yeagley (ref. 10) reported one test release in which homing pigeons carrying magnets were disoriented whereas controls carrying brasses were not; but neither he (ref. 11) nor other investigators (refs. 14 to 18) attempting to repeat his experiment ever obtained such results again. Moreover, several workers (refs. 19 to 28) who attempted to detect a sensitivity of birds to magnetic stimuli or to condition birds to respond behaviorally to such stimuli were unsuccessful.

Recently, however, Merkel and his colleagues (refs. 29 to 33) have claimed that European robins can orient in the absence of visual cues, and that predictable deviations in the robins' orientation can be produced by alteration of the magnetic field surrounding their cages; Perdeck (ref. 34) has attempted unsuccessfully to repeat these experiments. Southern (ref. 35) has reported a correlation between the accuracy of ring-billed gulls' orientation and fluctuations in the strength of the Earth's magnetic field. Graue (ref. 36) has mentioned that pigeons released near magnetic anomalies (total intensity) show more scatter in vanishing bearings than do similar pigeons released at sites with a normal magnetic field. Talkington (ref. 37) has claimed that pigeons tracked by helicopter exhibit a strong tendency to skirt around or head between magnetic anomalies. Several Russian workers (refs. 38 to 40) have reported a general increase in locomotor activity when birds are placed in artificial magnetic fields, and Reille (ref. 41) has reported success in conditioning pigeons to respond by heart rate changes to changes in the strength of an artificial magnetic field only slightly stronger than the Earth's.

In addition to these reports that birds respond to magnetic stimuli, there have been numerous claims that a variety of invertebrates exhibit orientational responses to artificial magnetic fields (refs. 42 to 52). Of particular interest is the recent demonstration by Lindauer and Martin (ref. 53) that terrestrial magnetism affects the orientation of the waggle dance of honeybees.

In view of these recent reports, and our own (ref. 54) demonstration that there is redundancy of cues in the pigeon orientational system, we reopened the question of whether magnets mounted on pigeons can affect the birds' homing behavior. Our early results are now available (ref. 65). This paper reviews those results, reports on some

more recent tests, and discusses possible implications of our findings.

METHODS

Each of our tests consisted of alternately releasing individual pigeons from two treatment groups. The birds for the two treatments were chosen randomly from a flock housed in a single pen, where they had experienced identical feeding, exercise, and training; in this way differences due to age, motivation, or physical condition were minimized. The birds of the experimental group wore a magnet bar glued, just prior to release, to the back at the base of the neck; the birds of the control group wore a brass bar of the same size, weight, and placement. In the early tests, the bars were approximately 2.5 × 0.64 × 0.25 cm and weighed between 2.7 and 3.2 grams; the field strength of the magnets at their poles averaged about 255 G (the field strength at 8 cm, at the bird's head, was about 0.45 G). In some of the later tests, bars measuring approximately 2.5 × 0.64 × 0.32 and weighing between 4.5 and 4.8 grams were used; the field strength of these magnets at their poles averaged about 600 G (1.1 G at 8 cm away). Neither of the two sizes of bars appeared to cause the pigeons any discomfort, and there were no detectable differences between the two sizes in their effects on homing behavior.

The birds were carried to the release sites in closed vehicles. They were tossed from the hand, the directions of toss being randomized. The release sites were carefully chosen to give clear visibility for a long distance in all directions. The observers watched each bird with 10 × 50 binoculars until it vanished from sight, and a compass bearing for the vanishing point was recorded to the nearest five degrees. The vanishing interval, i.e., the interval between toss and vanishing, was timed with a stopwatch. The time of arrival of each bird at the home loft was recorded, so that homing speeds could be calculated.

The circular mean for each group of vanishing bearings was calculated by vector analysis (ref. 55). The V test (ref. 56) was used to determine whether the bearings were significantly homeward oriented. The vanishing intervals and homing speeds of brass- and magnet-laden birds in each test were compared by means of the matched-pairs signed-ranks test (ref. 57).

For each series of tests, the bearings from the separate releases were also pooled, with the home directions all set to 0°. The pooled bearings were then tested for homeward orientation using the V test. When appropriate, the extents of scatter of the pooled bearings for the two treatments were compared by means of an F test proposed by Watson and explained in simple terms by Emlen and Penney (ref. 58).

TEST RELEASES

As far as one can tell from the literature, previous test releases of birds carrying magnets were all conducted on clear days. Since our experiments (ref. 54) had indicated that the orientation process used by pigeons on sunny days differs in some respects from that used on overcast days, we were particularly interested in finding out what would happen if birds carrying magnets were released under total overcast, when the Sun compass would be unavailable to them.

First, however, we conducted a series of tests (our series I) under Sun to determine whether we would get results like those already published by others. In all our releases of experienced birds from both familiar and unfamiliar sites at distances of 27 to 50 km (from north, east, and south), both the control birds and the experimentals were well-

oriented homeward, and in no case was there a significant difference between the two treatments in homing speeds. Figure 1 shows the pooled bearings from the six tests in this series; both the experimental and control birds are homeward oriented at $P<0.00001$. Thus these results agreed with those of other authors (refs. 14 to 18).

We now proceeded to conduct a series of similar tests (our series III) under total overcast, using experienced birds at sites where they had never previously been released; again the distances were 27 to 50 km. In five of seven tests the brass-laden birds were homeward oriented whereas the magnet-laden birds were not. Thus these five tests yielded results strikingly different from those obtained in the Sun releases. However, the other two releases in this series confused the picture somewhat—in one release both groups of birds were homeward oriented, and in one neither group was oriented. Figure 2 shows the pooled bearings for the seven releases in this series. The birds carrying brasses are homeward oriented at $P<0.00001$; the very large value of N for the birds carrying magnets has permitted detection of homeward orientation at $P = 0.02$ (Rayleigh test, $P = 0.06$). However, the bearings of the magnet-bearing birds are significantly more scattered than those of the brass-bearing birds ($P<0.005$).

Our results at this point seemed to indicate that magnets do not disorient experienced birds when the Sun is visible, but that they often do cause disorientation at unfamiliar release sites when the Sun is not visible. This could mean that the birds can use Sun cues and magnetic cues interchangeably, but that both together are seldom needed.

We had previously demonstrated that experienced pigeons can orient homeward under total overcast at unfamiliar release sites (ref. 54) but that first-flight birds cannot (ref. 59). The results discussed above now suggested that the experienced birds might be orienting under overcast by using magnetic cues as a substitute for Sun cues. But if this were true, why could not the first-flight birds do the same thing? We thought it possible that early training under sunny conditions is necessary to make pigeons responsive to magnetic cues, even though they can use Sun cues without prior training. To test this possibility, we put magnets or brasses on a large number of young birds when they first began to fly, and left these on throughout early training that consisted of a number of flock releases at distances of 1.6 to 16 km from all four cardinal directions. Some of the training flights were under overcast. Our earlier experience had shown that this was sufficient training to enable normal birds to orient under total overcast at distant unfamiliar release sites.

When the training was complete, these birds were used in a series of three test releases (our series V) under total overcast at a site 49.4 km south of the loft. Just before each bird was released, its magnet or brass was removed. Our thought was that the birds carrying brasses might have learned to use normal magnetic cues during their training, whereas the birds carrying magnets might not have been able to learn to do this. If this were so, then on their first single-toss flight under total overcast without magnets or brasses the birds that had until now worn brasses should be able to orient but the birds that had worn magnets should not. However, in each of the three test releases both groups were homeward oriented. Figure 3 shows the pooled bearings for the three releases in this series; both the experimental and the control birds are homeward oriented at $P < 0.00001$, and there is no significant difference in scatter between them. However, in

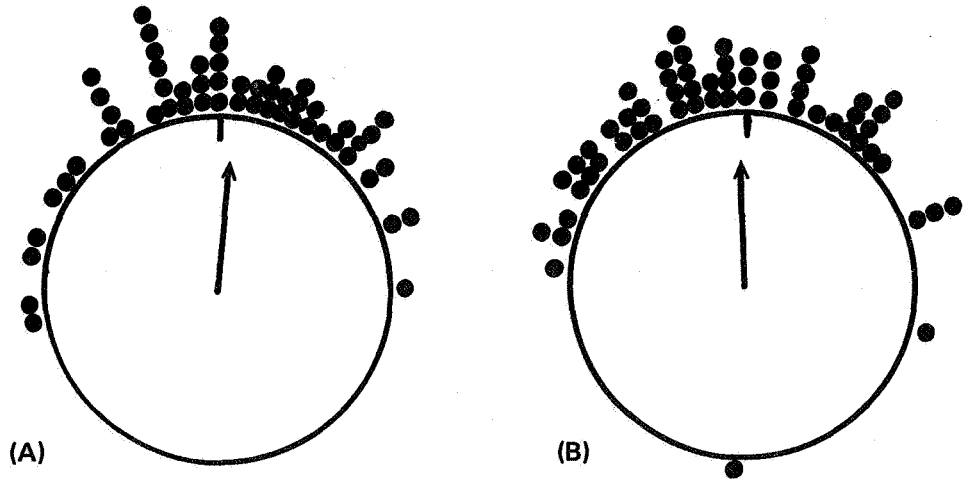

FIGURE 1. Pooled bearings from series I releases; experienced pigeons released under sunny conditions from distances of 27 to 50 km. Releases were from North, East, and South; home bearings have been adjusted to 0° (indicated by short line at the top of circle). The mean vectors are shown as arrows, with the maximum possible length of a mean vector (i.e., $r = 1$) represented by the radius of the circle. (A) Birds carrying brass bars, mean bearing 3°, $r = 0.738$ (homeward oriented $P < 0.00001$). (B) Birds carrying magnets, mean bearing 357°, $r = 0.727$ (homeward oriented, $P < 0.00001$).

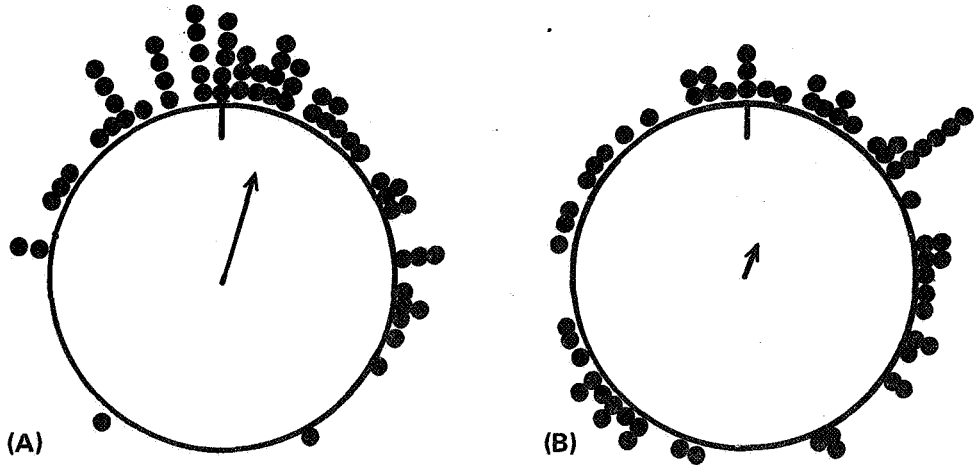

FIGURE 2. Pooled bearings from series III releases; experienced pigeons released under total overcast from distances of 27 to 50 km. Releases were from North and South; home bearings adjusted to 0°. (A) Birds carrying brass bars, mean bearing 17°, $r = 0.625$ (homeward oriented, $P < 0.00001$). (B) Birds carrying magnets, mean bearing 23°, $r = 0.211$ (homeward oriented, $P = 0.02$).

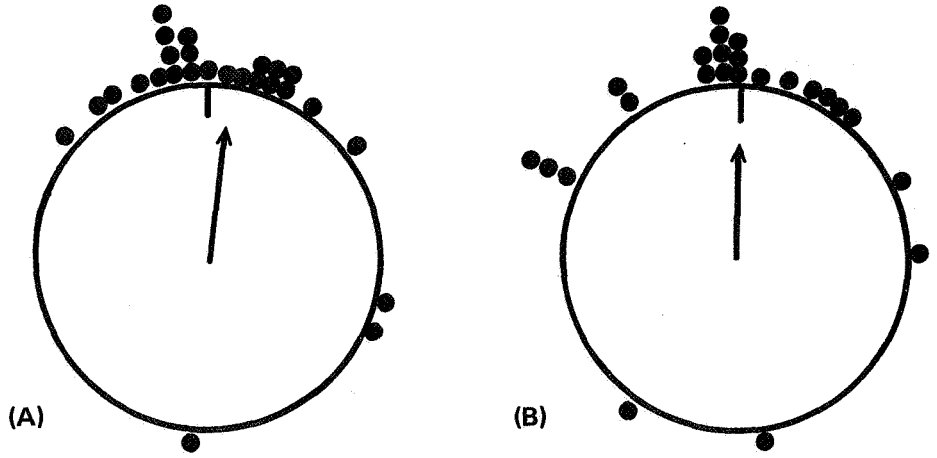

FIGURE 3. Pooled bearings from series V releases; from 49.4 km South under total overcast; home bearing adjusted to 0°. (A) Birds that formerly wore bars, mean bearing 6°, r = 0.761 (homeward oriented, $P < 0.00001$). (B) Birds that formerly wore magnets, mean bearing 0°, r = 0.657 (homeward oriented, $P \leq 0.00001$).

each of the releases the former magnet-laden birds took significantly longer to vanish. Thus, contrary to our expectations, the magnet-laden birds had apparently learned, during training, whatever is necessary to enable them to orient homeward under total overcast at an unfamiliar release site, but apparently the experience of wearing the magnets had made them slower in choosing their bearings.

We now had to reconsider our earlier ideas about the effects of training. Accordingly, we decided to look closer at the orientation behavior of first-flight pigeons. First we conducted a series of test releases (our series VI) under Sun, using first-flight youngsters only about three months old. In all three tests of this series (conducted from 26.7 km north), the magnet-laden birds vanished randomly whereas the brass birds were oriented homeward. Figure 4 shows the pooled bearings for the three releases in this series; the birds carrying brasses are homeward oriented at $P<0.00001$, whereas the birds carrying magnets are random, $P = 0.40$ (Rayleigh test, $P = 0.77$). The difference in scatter is significant at $P < 0.005$.

Since we had already shown that first-flight pigeons require the Sun for orientation whereas experienced birds do not (ref. 59), and the results of the series VI tests seemed to indicate that first-flight pigeons also require magnetic cues whereas experienced birds do not (see series I above), it seemed to us that perhaps training has the effect of making pigeons sufficiently adept at homing so that they can orient with less information than they need on their first flight.

However, this formulation soon proved to be much too simple. A series of six test releases (our series VII) under Sun using older first-flight birds (8 to 9 mo old) yielded mixed results. In three of these tests, the birds carrying brasses were oriented homeward whereas the birds carrying magnets were not, thus agreeing with the results of series VI. But in two tests both groups were homeward oriented, and in one test both groups were random. Thus it appeared that in some cases first-flight birds are not both-

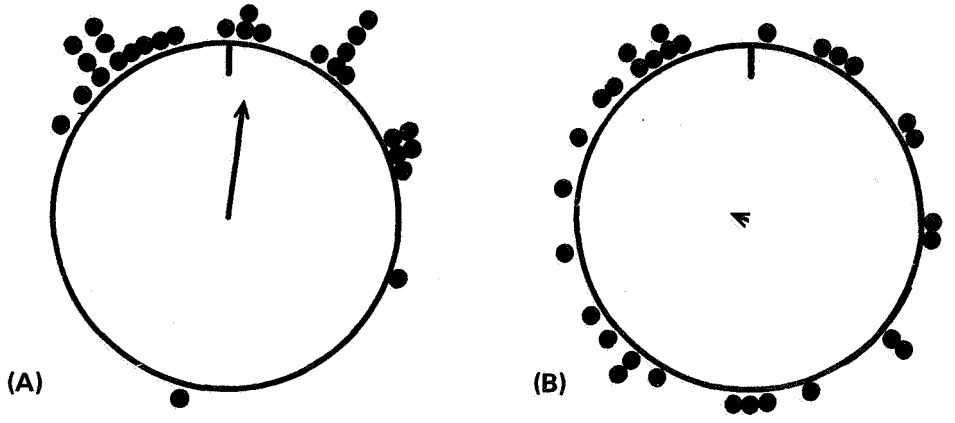

FIGURE 4. Pooled bearings from series VI release; very young first-flight pigeons released under sunny conditions from 26.7 km North; home bearing adjusted to 0°; (A) Birds carrying brass bars, mean bearing 7°, r = 0.669 (homeward oriented $P < 0.00001$). (B) Birds carrying magnets, mean bearing 290°, r = 0.094 (not homeward oriented, $P = 0.40$).

ered by magnets. Perhaps the greater maturity of the birds used in these tests is the reason, or perhaps it is the experience of more exercise flights at the loft.

Figure 5 shows the pooled bearings for the six releases in series VII. The birds carrying brasses are homeward oriented at $P < 0.00001$, whereas the birds carrying magnets are not, $P = 0.14$ (Rayleigh test, $P = 0.24$). One may question, however, whether the V test or Rayleigh test can legitimately be applied to the pooled bearings of the magnet birds, inasmuch as their distribution appears, on visual inspection, to be bimodal. The contrast between this distribution and that of the very young first-flight birds carrying magnets in the similar releases of series VI (fig. 4B) is striking, and raises the possibility that greater maturity has resulted in increased ability to detect the proper vector but that the magnets interfere with the choice of polarity.

Not only did the picture concerning first-flight birds become somewhat cloudy, but so did the picture concerning experienced birds released under Sun. The releases of series I had all been conducted at relatively short distances (27 to 50 km). When we conducted tests under Sun at greater distances, the results were different. One series of such tests (our series II) consisted of three releases from 84.5 km south, using experienced birds new to the site. In the first of these tests the magnet birds vanished randomly whereas the brass birds were homeward oriented (fig. 6A); the magnet birds also had significantly slower homing speeds. Although both groups of birds were homeward oriented in the second and third tests of this series (figs. 6B, 6C), the magnet-laden birds of both tests had significantly longer vanishing intervals, and the magnet-laden birds of the second test had significantly slower homing speeds.

In an attempt to determine whether magnets would cause a decrement in orientational or homing performance under Sun at comparable distances from directions other than south, we conducted two releases (our series VIII) from 73.5 km north, again using experienced birds, new to the site. In the first of these releases (fig. 7A), the brass-laden birds

were homeward oriented ($P = 0.002$) whereas the magnet-laden birds were not ($P = 0.077$). In the second test (fig. 7B), both groups were homeward oriented ($P < 0.0001$ for each). In neither release was there a significant difference in vanishing intervals or homing speeds.

If we look at the releases of series II and VIII combined, we find that in four of the five tests the birds carrying magnets exhibited a poorer performance than the birds carrying brasses, in at least one of the three variables measured (orientation, vanishing interval, homing speed). This seems to suggest that at longer distances magnets can affect the behavior of experienced pigeons released under Sun, just as magnets often affect the performance of first-flight birds under Sun at shorter distances (see series VI and VII). This conclusion appears to be valid only for birds new to the release site, however, because in a series of eleven tests (our series IX) under Sun from the same release site used in series VIII (73.5 km north), magnets had no detectable effect on birds with prior experience at the site (fig. 8), i.e. in none of these tests was there a significant difference between controls and experimentals in orientation, vanishing intervals, or homing speed. We plan soon to conduct test releases at distances of 160 to 320 km to check on the general applicability of these generalizations concerning the effects of magnets and of prior experience at the release site.

Having found that magnets often affect the performance of first-flight birds under Sun, even at short distances, and having learned that magnets sometimes affect experienced birds under Sun at longer distances, we decided to perform a series of releases (our series X) under Sun using young birds prepared the same way as in series V (i.e., trained in flocks up to 16 km in all directions, while wearing permanently mounted magnets

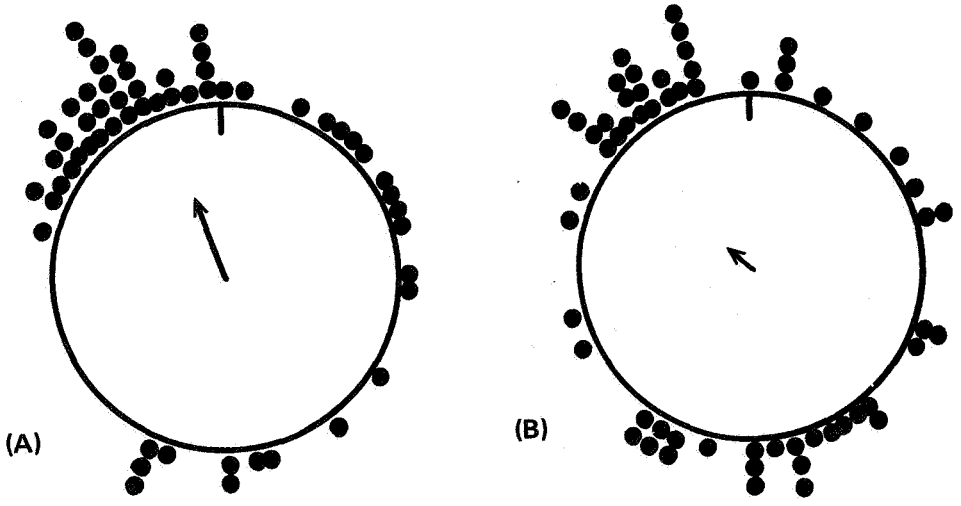

FIGURE 5. Pooled bearings from series VII releases; mature first-flight pigeons released under sunny conditions from distances of 27 to 50 km. Releases were from North and South; home bearings adjusted to 0°. (A) Birds carrying brass bars, mean bearing 340°, r = 0.475 (homeward oriented, $P < 0.00001$). (B) Birds carrying magnets, mean bearing 310°, r = 0.155 (not homeward oriented, $P = 0.14$).

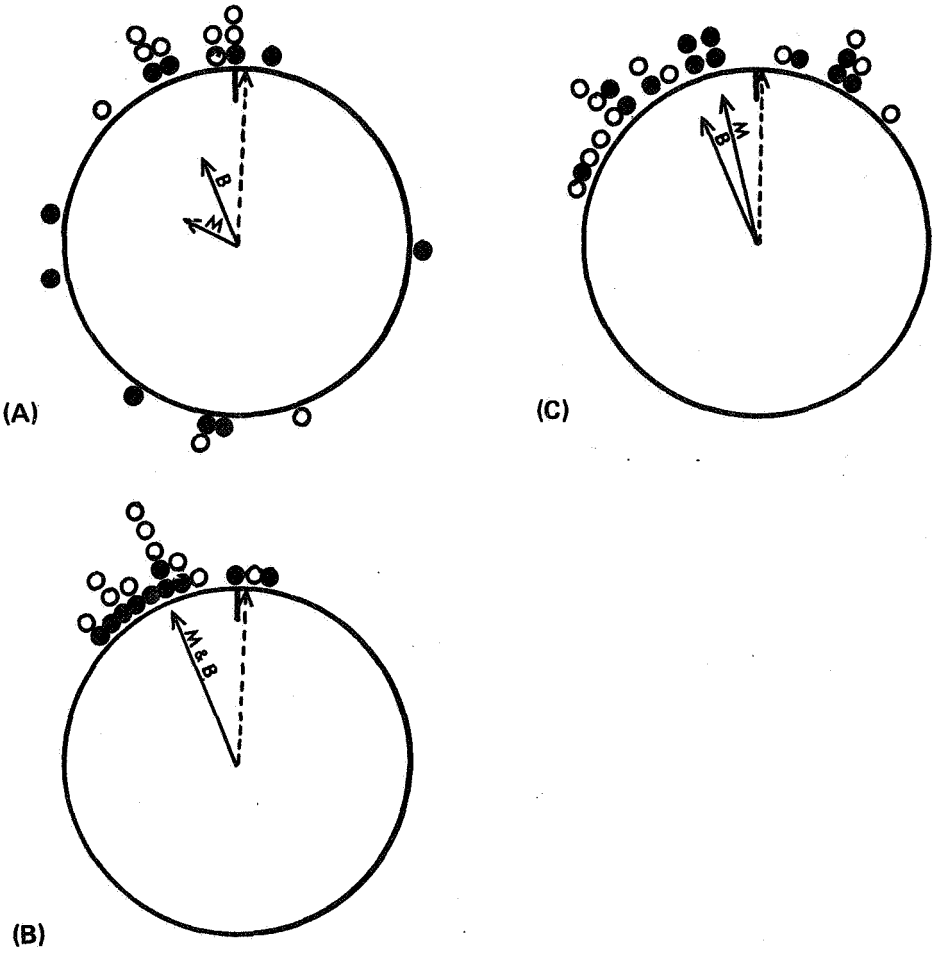

FIGURE 6. Series II releases; experienced pigeons, new to the site, released under sunny conditions from 84.5 km South. Home bearing (dashed arrow) is 3°; true North is indicated by short line at inner margin of top of circle. In figures 6 to 9, black symbols represent bearings of birds carrying magnets and open symbols represent bearings of birds carrying brass bars. (A) Release of May 20, 1970; mean bearing (B) of birds carrying brass bars, 341°, r = 0.584 (homeward oriented, $P = 0.009$); mean bearing (M) of birds carrying magnets, 291°, r = 0.231 (not homeward oriented, $P = 0.34$). (B) Release of May 21, 1970; mean bearing of brass birds, 337°, r = 0.972 (homeward oriented, $P < 0.0001$); mean bearing of magnet birds, 338°, r = 0.960 (homeward oriented, $P < 0.0001$). (C) Release of July 8, 1970; mean bearing of brass birds, 337°, r = 0.780 (homeward oriented, $P = 0.0005$); mean bearing of magnet birds, 350°, r = 0.865 (homeward oriented, $P < 0.0001$).

or brasses). All the tests in this series are being conducted from 73.5 km north. In some of these tests the magnets or brasses are taken off just before the birds are released, and in other tests the magnets and brasses are left on. In all tests performed so far, both

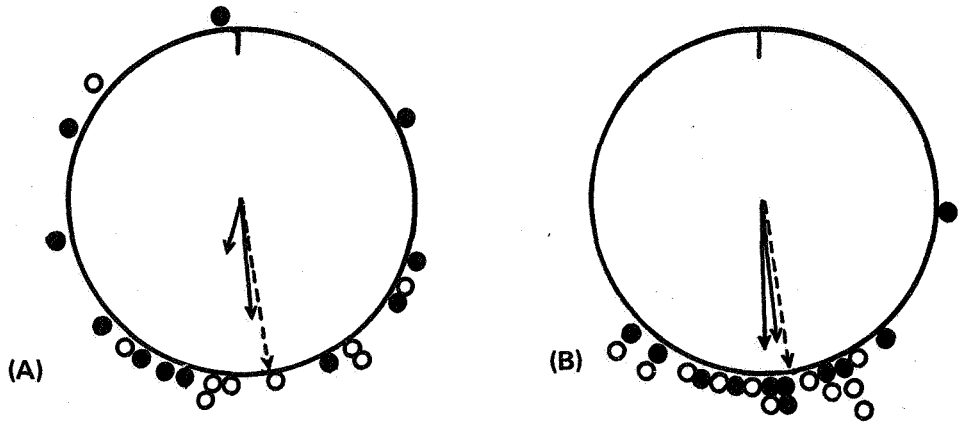

FIGURE 7. Series VIII releases; experienced pigeons, new to the site, released under sunny conditions from 73.5 km North. Home bearing (dashed arrow) is 173°. (A) Release of August 20, 1970; mean bearing of birds carrying brass bars, 177°, r = 0.691 (homeward oriented, $P = 0.002$); mean bearing of birds carrying magnets. 196°, r = 0.327 (not homeward oriented, $P = 0.08$). (B) Release of August 22, 1970; mean bearing of brass birds (longer arrow), 180°, r = 0.907 (homeward oriented, $P < 0.0001$); mean bearing of magnet birds (shorter arrow), 175°, r = 0.834 (homeward oriented, $P < 0.0001$).

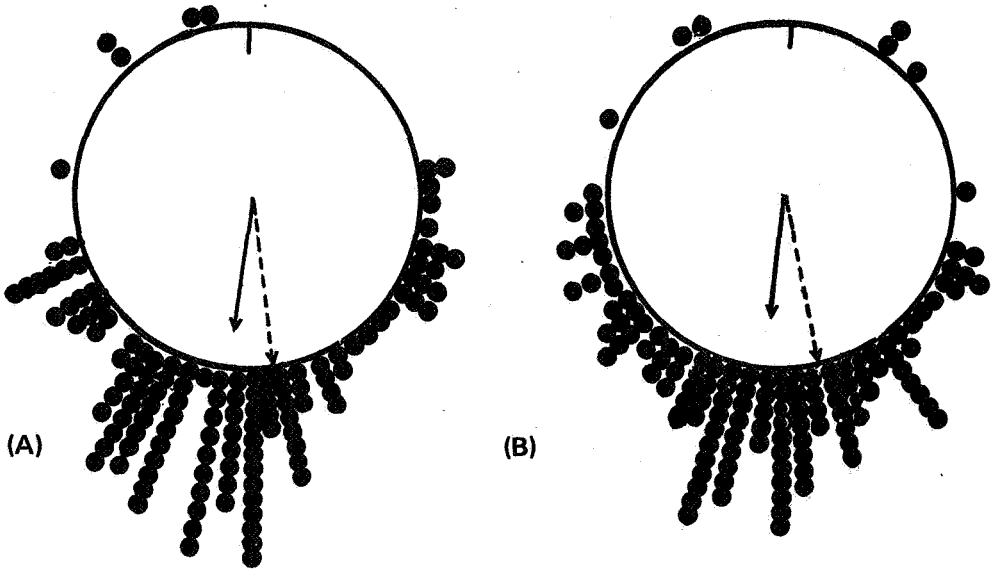

FIGURE 8. Pooled bearings from series IX releases; experienced pigeons, with prior experience at the site, released under sunny conditions from 73.5 km North. Home bearing (dashed arrow) is 173°. (A) Birds carrying brass bars, mean bearing 188°, r = 0.737 (homeward oriented, $P < 0.00001$). (B) Birds carrying magnets, mean bearing 191°, r = 0.721 (homeward oriented, $P < 0.00001$).

groups of birds have been homeward oriented, and in no case has there been a significant difference in vanishing intervals or homing speeds. Thus the apparent lengthening of vanishing intervals under overcast as a result of prior wearing of magnets, seen in series V, has not been found under Sun. Furthermore, the extensive experience of wearing magnets during short training flights may actually have made the birds better able to orient accurately while wearing magnets at distant unfamiliar sites; more tests, which we plan to conduct soon, should establish whether or not this tentative conclusion is true. Detailed data for this series will be published when all the tests have been completed.

Two other series of tests, recently begun, may be mentioned briefly. In the first of these, small circular magnets (1 cm diameter, 0.2 cm thick, 1 gram weight, field strength approximately 220 G) are glued to the top of the birds' heads; control birds wear brasses of the same size, shape, and weight. Figure 9 shows the bearings obtained in the first release in this series; the birds carrying brasses were homeward oriented ($P = 0.0002$), whereas the birds carrying magnets were not ($P = 0.12$).

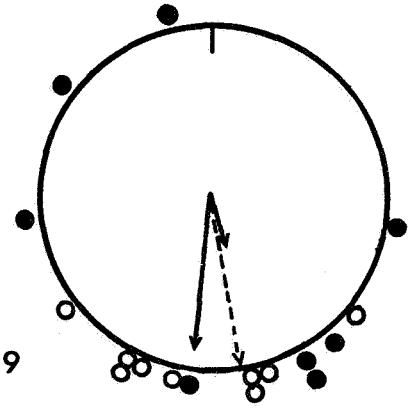

FIGURE 9. Bearings from test using magnets glued to birds' heads. Experienced birds, new to the site, released under sunny conditions, September 6, 1970. Home bearing (dashed arrow), 173°; distance, 73.5 km. Mean bearing of birds carrying brass bars (longer solid arrow), 184°, r = 0.879 (homeward oriented, $P = 0.0002$). Mean bearing of birds carrying magnets (shorter solid arrow), 168°, r = 0.294 (not homeward oriented, $P = 0.12$).

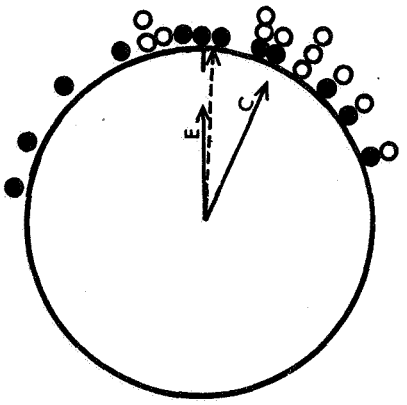

FIGURE 10. Bearings from test using birds wearing Walcott-type electromagnets. Experienced birds, new to the site, released under sunny conditions, August 20, 1970. Home bearing (dashed arrow), 3°; distance 84.5 km. Bearings of control birds wearing nonfunctioning electromagnets are represented by open symbols, bearings of experimental birds wearing functioning electromagnets by black symbols. Mean bearing (C) of control birds, 25°, r = 0.901 (homeward oriented, $P < 0.0001$). Mean bearing (E) of experimental birds, 1°, r = 0.723 (homeward oriented, $P = 0.0003$).

The second of these recently begun series is an attempt to repeat the tests using electromagnets reported in this volume by Walcott. Unfortunately, in the one such test we have performed so far (fig. 10), our results differed from those of Walcott; both the experimentals and the controls were homeward oriented and there was no significant difference in vanishing intervals or homing success. We plan much more tests as soon as we have redesigned the apparatus so as to cause less discomfort to the birds.

DISCUSSION OF RESULTS

Our test releases provide evidence that under certain conditions magnets can cause confusion to homing pigeons. If we consider only those tests in which the birds of one group were homeward oriented and the birds of the other group were not, we find that in all 13 such cases it was the brass-laden birds that were oriented and the magnet-laden birds that were not. The binomial probability (one-tailed) of getting such results by chance alone is only 0.0001. Similarly, in all five tests where there was a significant difference in homing speeds, it was the magnet-laden birds that were slower; the chance probability of this is 0.031. In all eight tests in which there was a significant difference in vanishing intervals, it was the magnet-laden birds that took longer; chance probability, 0.004. Or if we examine the results in another way, and consider all releases in which there was a significant difference between the two treatments in at least one of the three variables measured, we find 21 such releases, and in all cases it was the magnet-laden birds that exhibited the poorer performance; the chance probability of such results is considerably less than one in a million.

It seems unlikely that these results are due simply to some general disturbing effect of the magnets, since the effects of the magnets differ depending upon weather conditions, the previous training of the birds, and whether or not the birds have had prior experience at the release site. I think it more likely that the magnets have a direct effect on the orientational mechanisms used by the pigeons. It is important to point out, however, that our results do not provide direct proof that pigeons can use magnetic cues in homing, though that is of course one possible implication. Another possibility is that some component or components of the orientation system, important under certain conditions but not under others, fails to function properly in the presence of a magnetic field as strong as that imposed on the birds by the magnets we used. We hope soon to be able to evaluate these alternative possibilities.

For the sake of argument, the rest of this discussion will assume that the first of the two above-mentioned interpretations of our data is correct, i.e. that pigeons are capable of using magnetic cues as one component of their orientation system.

A first question that comes to mind is what might be the mechanism whereby a pigeon could detect magnetic cues. Unfortunately, no convincing answer is yet available. Both Yeagley (ref. 10) and Talkington (refs. 12 and 13) have hypothesized that a bird's movement through the Earth's magnetic field might result in an induced electromotive force, which might then be detected. However, even if one assumes an optimal situation (e.g. flight at 64 km per hr, with the cross-sectional area of the bird cutting the lines of magnetic force exactly at the perpendicular), the most optimistic estimate of the induced emf is on the order of 1 mV per cm; an estimate on the order of 1 μV per cm is probably more realistic for the required sensitivity of the bird's sensory apparatus if directional information is to be obtained. Not only is this an extremely small value, but its calculation disregards the point made by several authors (refs. 60 to 62) that the electric fields resulting from motion through a magnetic field cannot be distinguished from uniform static fields; since the electrostatic field of the Earth's atmosphere is on the order of 1 V per cm, but quite variable, it follows that it is exceedingly unlikely that a pigeon could detect, against this background, the minute superimposed voltage resulting from its movement through the Earth's magnetic field.

Another possibility was suggested by

Stewart in 1957 (ref. 63), but has been largely ignored (a hypothesis nearly identical to that of Stewart was suggested to me in February 1970, by Robert R. Capranica of Cornell University; at that time, neither Capranica nor I was aware of Stewart's paper). As a bird flies through the atmospheric electric field, an electrostatic field will build up on its surface, just as it does on an airplane. This makes the bird, in effect, a moving electric charge. Now, such a moving charge will be surrounded by its own magnetic field. The Earth's magnetic field and the magnetic field around the bird should then interact to produce a torque on the bird, which the bird might detect. However, even under the most optimistic assumptions, calculations indicate that the torque would be on the order of only 1 dyne.

It is therefore understandable that Stewart's hypothesis has been dismissed, since at first glance it would seem unlikely that a flying pigeon could distinguish so small a torque against a background of the numerous other torques it must be experiencing from wind and atmospheric turbulence. But there are at least two reasons why Stewart's hypothesis should receive some consideration here. First, it has recently been shown that feathers exhibit piezoelectric properties, twisting when exposed to electric stress, with the degree of twist proportional to the strength of the electrical excitation (ref. 64). Receptors in the feather sockets might measure this twist, thus enabling the bird to measure, indirectly, both the electrostatic field on its feathers and the surrounding magnetic field. Given this information, the potential for deriving information concerning the Earth's magnetic field from the torque experienced by the bird is considerably enhanced. Second, sensory physiology provides numerous examples to substantiate the generalization that organisms have evolved remarkable abilities to separate signals from noise whenever the signals have been really important to them. Therefore we should not be too hasty in dismissing hypotheses based on birds' detection of very weak signals.

Having given reasons for reconsidering Stewart's hypothesis, however, I must now say that, if birds can detect weak magnetic stimuli, it seems to me likely that the detection is based on some direct effect of the magnetic field on the sensory apparatus of the organism, rather than on an induced emf or the sort of indirect process discussed in the preceding paragraph. One possibility would be actual mechanical displacement of some structure, in the way that gravity causes displacement of the otoliths or vibrations cause displacement of the cilia of hair cells in the cochlea. In this regard, it is pointed out that the displacement necessary to result in a generator potential need not be great; in the cochlea, for example, movement of the cilium of a hair cell through a distance less than the diameter of a hydrogen atom is sufficient to initiate impulses in the auditory nerve fiber. However, mechanical displacement is not the only possible way in which magnetic fields might have a direct effect on some sensory apparatus; another possibility would be the alteration of molecules or atoms in sensory cells. This might be a molecular change similar to that produced by light in photoreceptors, or perhaps (to be even more daring) a nuclear magnetic resonance effect.

My intent here is not to espouse any one particular hypothesis for detection of magnetic fields, but simply to emphasize that if organisms can detect magnetic stimuli (and the paper by Lindauer in this symposium appears to add greatly to the probability that honeybees, at least, can do this), then the detection mechanisms for which we must seek may well involve processes different from those most frequently suggested in the past.

Magnetic stimuli differ considerably from most of the kinds of stimuli we normally think about; for example, there is no reason to assume that the receptors will be on or even near the surface of the body, since magnetic fields pass through the body. Thus the receptors could be anywhere inside the animal, for example in the brain itself.

However, even if future research conclusively demonstrates that pigeons use magnetic cues in orientation, it is my conviction that we will still be far from a complete understanding of the pigeon navigation system. It seems likely that magnetic cues, like the Sun compass and, perhaps, landmarks, constitute only one element in an exceedingly complex and redundant system. Witness the disturbing variability found in the results of the tests reported in this paper—until we can explain why magnets caused disorientation in some tests but not in others, even when weather conditions, prior experience of the birds, and all other readily apparent variables were held constant, we have a long way to go. Take, for example, the two releases shown in figures 6A and 6B. The field observers reported a strong subjective impression that the birds in the figure 6A test showed two quite different behavioral patterns—only two of the 10 brass-laden birds ever entered the southern half of the sky, whereas all of the 10 magnet-laden birds spent a major portion of their circling time in the southern sky. By contrast, in the test of figure 6B, the same observers had the impression that all the birds belonged to one behavioral group—no bird from either treatment entered the southern half of the sky, and most flew off toward home with no circling. Yet the birds used in these two tests were drawn at random from the same pen, were of the same age and breeding, and had had identical training. Furthermore, the two tests were conducted on consecutive days under what appeared to be nearly identical wind and weather conditions. Why, then, did the two tests yield such different results? I am led to the conclusion that in addition to Sun, landmarks, and perhaps magnetism there remain other important cues that we must discover before we can put the pieces together to produce a satisfying description of the pigeon navigation system.

As a further example of the sort of evidence that leads me to this conviction, let me mention briefly a clock-shift test (six hours fast) that we recently performed under sunny conditions. This release was from a site 33.5 km east of the loft, a site from which we had made more than 50 previous releases, with the mean bearings of normal birds always being well oriented homeward. Furthermore, we had conducted many previous clock-shift tests at this site under sunny conditions and had always obtained a homeward-directed mean vector for the control birds and a southward-directed mean vector for birds clock shifted six hours fast. Yet on this particular day the control birds vanished nonrandomly northward (353°) and the shifted birds westward (266°). In other words, the mean bearings of the two treatments differed by roughly 90° (actually 87°), as expected, but both means were rotated nearly 90° clockwise from the predicted directions. We could detect no odd conditions of wind or weather, and the K values reported by the government indicated no unusual magnetic activity that day. Yet something appeared to have rotated the navigational grid of our birds, affecting both treatments in the same manner so that they maintained the expected relationship to each other.

Though we do not yet know all the cues used by a navigating pigeon, we can begin to say something about the relative importance of the cues we do know. Numerous workers, among them my own group (ref. 54), have

shown that clock-shifted pigeons released under Sun vanish at roughly the predicted angle relative to the controls even when released at sites from which they have flown many times before. Thus it seems established that the Sun compass is at a higher level in the hierarchy of cues than landmarks. Since our tests indicate that magnets have no effect (short distances) or only a small effect (long distances) on experienced pigeons released under Sun at unfamiliar sites, we can probably safely conclude that the Sun compass also ranks higher in the hierarchy of cues than magnetism. When the Sun-compass information and familiar landmarks are both available and are in agreement, magnets appear to have no disturbing effect on experienced birds even at long distances (fig. 8); in other words, Sun and landmark cues together can completely eliminate any effects of magnetic cues. We have so far conducted only a few tests using experienced pigeons carrying magnets released under total overcast at familiar sites, and cannot therefore make any final statement about the relative importance of familiar landmarks and magnetic cues; however, our tentative impression is that magnetic cues rank higher than familiar landmarks, at least at distances of 32 kilometers or more.

All of the above speculations about the hierarchy of cues in the pigeon navigation system apply only to experienced birds. The tests discussed in this paper, and others (not involving magnets) to be published elsewhere, suggest that the various cues interact in quite different ways in first-flight pigeons. Perhaps detailed comparisons of the orientational behavior of first-flight and experienced pigeons will help us discover additional cues or cue interactions, and will permit us someday to begin to see at least the outlines of a unifying theory to explain the intriguing mystery of pigeon homing.

ACKNOWLEDGMENT

I extend my thanks to David H. Niver, Andre Gobert, Irene Brown, Jerry F. Downhower, Lorraine Pakkala, Deena Zalkind, Barbara Cobey, Judith R. Alexander, Melvin Kreithen, and Robert Capranica, all of whom helped with releases or contributed suggestions or both. Donald M. Windsor conducted all the releases in series IX. Research supported by grant GB–13046X from the National Science Foundation.

DISCUSSION

GALLER: Have you tried (1) comparing brass-laden birds with brass-laden birds and (2) using bar magnets on one set of birds and degaussed steel on the other set?

KEETON: (1) We have done brass versus brass, and also brass versus birds wearing nothing; there is no difference. In other words, the weight of the bars doesn't appear to cause any difficulties. In all the tests shown in the figures, the controls were wearing brass bars equivalent to the magnet bars in size and weight. However, our tests indicate that we could do just as well with control birds wearing nothing. (2) We have considered it, but have not yet done it. The use of the Helmholtz-coil technique (mentioned by Walcott) gives a more uniform field than just bar magnets. On the other hand, the coils introduce a great deal more abnormal behavior on the part of the bird, because the birds decidedly dislike the apparatus. We are trying to build coils that can be controlled from the ground by radio, so that we shall be able to turn them on or off or vary the field strength at will.

GRIFFIN: All of this recent evidence on magnetic effects is very impressive. But I am not sure about your last point, that new and not yet identified sensory channels must be involved. This appears to me a situation where the variables are not yet all controlled. But an uncontrolled variable does not necessarily mean a wholly new sensory modality.

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CLOSING SESSION

A Look into the Future

Chairman, KLAUS SCHMIDT-KOENIG

A Look into the Future

SIDNEY R. GALLER
The Smithsonian Institution

I WOULD LIKE TO PRESENT a different perspective on biological orientation and navigation research. I feel as if I had been away on a long recess and returned to find the same faces and for the most part the same topics. Happily, I note that there have been some exciting advances in this field.

This symposium recalls to mind several historical landmarks in the development of the field of biological orientation and navigation that might be considered as bench marks for plotting the future directions for research.

I would like to remind the senior scientists among you who have been in this field since its modern beginning that this meeting takes place almost 23 years after the first federal contract for research in biological orientation.

Further, it marks the 20th anniversary of the first federal research program in biological orientation; and it comes on the heels of the 17th anniversary of the first conference on animal orientation in 1953.

It occurs 12 years after the first telemetered satellite experiment which carried yeast cells in a device for measuring CO_2 production as a primitive biological rhythm indicator.

It comes one decade after the first landmark study and report on the relevance of biological orientation to space flight sponsored by the National Research Council Committee on Bioastronautics (the forerunner of the National Academy of Science's Space Science Board).

It comes a decade after the first Cold Spring Harbor Symposium on biological clocks, and 8 years after the first Interdisciplinary Conference on Telemetry in Animal Behavior and Physiology in Relation to Ecological Problems held in March 1962.

It takes place 7 years after the establishment of the Bioinstrumentation Advisory Council of the American Institute of Biological Sciences.

And finally, this meeting is being held one year after the NAS Santa Cruz review of NASA's biosciences program, which recommended special emphasis on biological orientation and navigation research. I am pleased to see a number of scientists who participated in Group V of that summer study here today.

After listening to a number of extraordinarily interesting presentations and discussions during this symposium, I am led to conclude that although there have been an impressive number of advances in our understanding of the underlying mechanisms of orientation and navigational phenomenology, there continues to be a direct correlation be-

tween the limitations on our knowledge and the constraints on our plans to observe orientation behavior and to interpret its significance under natural field conditions.

Stated more succinctly, today, more than two decades after the official genesis of this field, we continue to be limited much more by the lack of instruments and techniques than we are by the paucity of scientific interest and ability.

Let us recapitulate the financial history. From that first study 23 years ago, costing approximately $15 000, the Navy and then, subsequently, the Air Force Office of Scientific Research, increased support to a peak of approximately $300 000 by 1965.

From 1965 on, the amount of support for this important field from Department of Defense agencies dropped off dramatically to a low of $73 000 in 1969. However, beginning in 1960, NASA investment increased from approximately $50 000 to a peak of $1.4 million in fiscal year 1969 (not including instrumental support). These figures, incidentally, are rough estimates.

Unfortunately today, fundamental research in NASA's bioscience program is almost extinct, and the future support picture for this kind of research is dismal.

At the same time, we, as a group of specialized scientists, long ago reached the point of becoming dependent on very expensive, sophisticated instrumental support. Today we need mechanisms for stabilizing financial support, for instrument development and utilization, and for data gathering and redistribution that transcend the interests of any single agency in the United States and abroad.

Indeed, if ever there was a field of biological science that depended on international cooperation, both in carrying out experiments and in gathering data, it is the field of biological orientation and navigation.

I hope that before we leave today we can agree on the next steps to be taken in overcoming the financial limitations and in anticipating the needs of the coming generation of investigators through an international plan of action.

Permit me to set the stage for the next steps by examining some of the happenings of the past.

First, just for fun, let me quote from the late Theodore Schneirla's introductory statement to the First Conference on Animal Orientation back in February 1953.

> A conference on this topic [animal orientation] should benefit our interpretive techniques and theoretical insight. Orientation study is characterized by a tentativeness and often an immaturity in theoretical grasp of problems. The reason for this certainly is not simple. It is true that many separate and very different lines of investigation have been developed. Some of the investigations fronts have reached a relatively high degree of specialization, but, on the whole, without a parallel theoretical development along broad phyletic lines. Orientation of specialists is commonly much too partitive.
> Specialists in the study of orientation along different lines, not infrequently carry out their work without much attention to other investigations with different organisms. Not a few seem to believe that they can select their problems, investigate them, and interpret their results without being much distracted by theory.
> What may be gained and what may be lost through this point of view is a sufficiently important question to warrant a careful group stocktaking by interested specialists from fields as different as those represented in this conference.

I submit that the fields today are in many ways just as different as they were in 1953.

Next, let me quote from the 1960 landmark report of the Biological Orientation and Navigation Panel of the Armed Forces National Research Council Committee on Bioastronautics.

> The cues or coordinates for long-range annual migration and homing are not understood. The sensing devices and the integration of sensory input relevant to those be-

> havioral achievements are proper subjects for investigation.
> Sensory physiological investigations and analysis of communication behavior are essential for continued progress in this field. There exists a requirement for accelerating the development of instruments and techniques necessary for the biophysical characterization of integrated systems of biological orientation.

Later on in the panel's recommendations:

> Specifically, the panel emphasizes the need for the establishment of national centers to develop classes of instrumentation and techniques which can be used for a quantitative description of biological systems.
> In addition, the panel recognizes the need for establishing centers that will be useful in the development of new drugs and the procurement of new species of animals for biological experiments. It is envisioned that such centers would receive direct support from sponsoring organizations thereby freeing the biological scientists from the need to expand research budgets for this type of activity.

And, finally:

> The panel makes the strongest recommendation in regard to the need of biological scientists for aid and facilitation in the procurement of specialized equipment, materials and methods.

That report led directly to the first interdisciplinary conference on the use of telemetry in animal behavior and physiology in relation to ecological problems which was convened March 28 through 31, 1962.

Subsequently, it led to the establishment of the Bioinstrumentation Advisory Council in the American Institute of Biological Sciences, to serve as an "honest broker" between biologists with requirements for measurements, and instrumentationists with the capability of satisfying those requirements, converting requirements into specifications to guide the instrumentationists.

Most recently, at the Santa Cruz meetings, members of Group V spoke of the need for coordination centers and group systems. Permit me to quote some of the comments of Group V:

> The requirements for ground support of animal tracking activities are illustrative of the needs for a central communication and coordination organization. An optimum ground support system should incorporate the following capabilities:
> 1. A means to bring biologists into contact with expert technical consultants who can help them translate their scientific needs into technical design;
> 2. A laboratory facility to develop the prototype sensors, transducers, transmitters, transponders, receivers and other equipment for studying the biology and behavior of test animals; and,
> 3. A network of both fixed and mobile monitoring stations that would receive data telemetered either from the animals or from satellites. These stations would serve also to gather environmental and ecological data.

And then, finally, let me quote the key recommendations:

> We recommend that a satellite be instrumented to establish and maintain contact with free ranging animals in order to determine their special position, to collect information from sensors they carry, and to relay these data to ground centers for biological analysis.
> We recommend and place high priority on the development of miniaturized electronic devices or platforms to be mounted on free ranging animals that will fix the geographic position of the animal, monitor relevant aspects of its environment and determine its physiological state.

And so, where are we today? I think there is an opportunity for a group—let's call it a self-constituted committee—to come together to draft some sort of an action plan for the establishment of a centralized facility, or a series of them, which would serve as a source of engineering advice for biologists. This plan should be published in the appropriate journals where it would be reviewed and evaluated by the international biological sciences community. Subsequently, it could serve as a basis for seeking financial support,

not only in the United States, but from all over the world.

I would like to sketch one such plan. I do not offer it as a solution, but only as a point of reference.

I start with the premise that no single institution, by itself, could have the spread of intellectual interests or of resources needed to sponsor this kind of an effort.

I also offer the premise that the best way to manage such an organization would be through a consortium of academic institutions.

Now, I submit also that support for what follows could come from several kinds of sources:

(1) From private organizations—in the form of grants or gifts

(2) Public groups in the United States, federal organizations, and groups abroad

(3) Commercial sponsors—offering either currency or equipment as gestures of good will

At the operating level, I visualize an organization that is tripartite, consisting of instrumental systems development, data management, and research facilities.

Under the *instrumental systems development,* I visualize an arrangement like BIAC (the AIBS Bioinstrumentation Advisory Council) where biologists with data requirements, but without competence in determining their instrumental needs, could come and have their requirements converted into instrumental specifications.

At this stage the specifications (or other information) could either go back to the requester—who could then submit the specified design wherever he pleased, or it could go to his university engineering facility—which could then build the equipment, or the biologist could ask this organization to contract for development of the instruments. In a U.S. agency, it could be built inhouse, in a research, development, test and evaluation facility. The proposed facility, devoted to applied research, development, test and evaluation, would end up developing a low-cost, high-quality, mass producible instrument for biological research.

Under *data management* I see data collection from satellites, either in real time or stored time, their collation as appropriate, their storage, retrieval, and distribution. Implicit in this plan, of course, are some pretty expensive machines, not only for data gathering, but for programming.

And finally, *a research laboratory or a research facility* with a core group of scientists and instrumentalists and with facilities for a large number of visiting scientists. This laboratory would be the real heart of the works. It would be the equivalent of a kind of MBL-like arrangement, where visiting scientists could come and take advantage of a unique instrumentationist facility and a data gathering facility.

I would like to end up by pointing out that there is a special reason why this is not only timely, but urgent. First, the International Biological Program is supposed to be involved in international data gathering and would benefit greatly from this kind of facility. More urgent, and more important in the United States, at least, is the growing interest on the part of NASA and other federal agencies in adapting space technology to environmental studies. The Earth Resources Orbiting Satellite Program is an example. Here a group of interested scientists and engineers from several federal agencies, including NASA, the Department of Commerce, and the Department of Interior, and I believe the Department of Agriculture, have decided that they need certain kinds of data to be gathered from orbiting satellites using a whole

system of sensors and telemeters, many of which have not as yet been evolved.

I must enter a caveat here, however, because it seems to me that what the satellite group is really asking for is a body of applied data for resource management. We have to be careful that no one confuses this kind of programmatic requirement with the need for fundamental biological data on behavior, psychophysiology, and ecology.

If we are not careful, there is reason to believe that this confusion will be compounded and we will find ourselves in the same situation that existed a decade ago, when oceanography developed into an active field. It was automatically assumed that the marine biologists would get their fair share of the facilities, the instruments, and the dollars that suddenly became available, but in point of fact, most of the investment was in geophysics or physical oceanography by virtue of the interests of some of the principal supporting organizations.

I believe there is now opportunity and equipment to follow up on the recommendations that were made in the early 1950's and again at the Santa Cruz meetings to arrive at a consensus and that could serve as the basis for seeking support from a variety of organizations, internationally.

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